MOVEMENT OF ADDED NITROGEN AND PHOSPHORUS IN A PINE FOREST ECOSYSTEM

By

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To my wife

Tiffany

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MOVEMENT OF ADDED NITROGEN AND PHOSPHORUS IN A PINE FOREST ECOSYSTEM

By

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Chairman: Dr. W. L. Pritchett
Major Department: Soil Science

The movement of N in an 11-year-old slash pine forest ecosystem was followed over two growing seasons, using ammonium sulphate fertilizer labelled with 2.388 atom percent ^{15}N. The N fertilizer was applied at 0, 56, and 224 kg N/ha. The initial uptake of ^{15}N and ^{32}P (applied as concentrated superphosphate) was followed in two trees, for a period of 71 days.

The first indication of the isotopes in the foliage was 5 to 7 days after their application to the surface of the litter. Dry weather was responsible for the delay in ^{32}P uptake, but it was not clear if this was the only reason for the delay in ^{15}N uptake. Both isotopes moved in greater quantities and were in higher concentrations in the lower crown foliage. The pattern resulted from mass flow in the transpiration stream and a dilution effect from reserves stored in the crown. The ^{15}N levels were higher in the current foliage than in the older foliage, presumably as there was a higher demand for N in this rapidly growing foliage. In contrast, the ^{32}P was higher in the older foliage.

the reason for this was not definitely established, but it may be related to a demand for P associated with high Al levels in the older foliage. The uptake of ^{32}P was linear with time after the 3rd week; the ^{15}N uptake was most rapid between the 3rd and 6th week.

In the second growing season there was a 50 percent decline of total N and in ^{15}N in the previous seasons flush of needles. This was associated with transfer to newly developing tissues. The movement of P from these needles was less marked. In late autumn and winter dry weight and N content of all needles increased.

Most of the tagged N moved rapidly through the litter in the first weeks after fertilization. There was also downward movement in the topsoil. The total amount of labelled N in the soil declined rapidly in the first 12 weeks, with little subsequent change after that date.

The amount of labelled N in the roots and above-ground parts of the trees at harvesting (19 months after fertilization) was 1.6 and 8.9 percent of the total amount applied. The recovery was the same in both the low- and high-N treatment. Of the amount recovered in the above-ground parts of the tree 48, 36, and 16 percent was in the foliage, stem, and branches, respectively. The highest levels of ^{15}N were associated with the metabolically active regions, i.e., the foliage, buds, branches, and wood formed since fertilization.

Some 50 percent of the ^{15}N applied could be accounted for at the end of the second growing season. The sample trees

contained 10 percent of the applied N, the surrounding trees 15 percent, and the litter and soil about 25 percent. The low recovery was associated with the open nature of the system. Part of the loss was probably associated with litter fall. Leaching and denitrification may also have occurred.

INTRODUCTION

In the last 25 years there has been widespread interest in forest fertilization. This has followed a switch in emphasis from the exploitation of natural forests to intensive plantation management techniques. The species or genotypes now being employed are not always adaptable to their new soil environment. In addition, intensive cultural practices and genetic selection favor higher production and increased nutrient demand. The potential for economic use of fertilizers in forests has stimulated current research in this area.

The commercial use of fertilizers in forests exceeds 250,000 ha/year (Hagner)[1] and is a direct result of tree nutrition research. In the Southeastern Coastal Plain (USA), commercial fertilization is mainly with phosphates applied to young pine trees growing on poorly drained sands. Early experiments on these sites demonstrated that phosphorus (P) was the main nutrient limiting growth and that excellent growth responses could often be obtained (Pritchett and Llewellyn, 1966; Pritchett and Smith, 1970). More studies indicated that the addition of other nutrients to some soils may also improve growth and that responses may be obtained in older plantations (Pritchett, personal communication).

To develop a sound basis for forest fertilization it is important to understand the fundamental processes connected with tree nutrition. Of particular importance are processes involving the soil, the plant, and their inter-relationships. Obviously many concepts and practices may be based on, or extrapolated from, the wide experience and research with agronomic and other speciality crops. However, forest ecosystems, and the trees themselves, have unique characteristics and it is on these traits that tree nutrition research is needed.

The large size of trees necessitates the movement of water, minerals, and foods over great distances. Root systems are often deeper, have the capacity to use less available nutrients, and also may become grafted to neighboring trees. Trees have long life spans which influence their biomass and nutrient accumulation patterns. They have lower elemental concentrations of nutrients in their tissues than most agronomic plants and exhibit internal nutrient cycling which reduces the demands on the soil.

In a forest ecosystem nutrient cycling is an extremely important nutritional factor. These cycles are often relatively complex, involving several subordinate biological and geochemical cycles of varying time periods. The systems are not necessarily closed.

In forests, particularly those dominated by conifers, soil conditions are different from those found in agronomic situations. Thus, forest soils are seldom limed and may be

quite acid. This influences soil-fertilizer relationships, nutrient availability, nutrient leaching, and microorganism populations. A well-developed litter layer is often present. This layer has distinct microorganism populations and modifies nutrient and water availability.

The development of the symbiotic ectomycorrhizal association with pines is known to have considerable importance in the nutrition of these trees. The association between the fungus and the plant root enables the tree to thrive under low nutrional conditions.

Thus, it is difficult to predict from knowledge gained with agronomic crops what the fate would be of fertilizer applied to a stand of trees. The primary concern of this study is the movement of nitrogen (N) and P in a pine forest ecosystem. The objectives were to study:

1. The initial uptake of fertilizer applied N and P into the trees' crowns.

2. The long-term movement of N into the tree and its distribution internally.

3. The uptake of N as related to rate of ammonium sulphate fertilizer application, and its distribution within the tree and other parts of the ecosystem after two growing seasons.

4. The movement of N from fertilizer, through the litter and soil.

The results obtained, together with information and principles from forestry, soils, and related sciences, should

help provide a basis for rational fertilizer use in pine forests.

NOTES

[1]Hagner, S. 1971. The present standard of practical forest fertilization in different parts of the world. Paper presented before Sec. 32, XV IUFRO Congress, Gainesville, Fla. 16 p.

LITERATURE REVIEW

N and P Fertilization of Forests

The potential for forest fertilization on the Lower Coastal Plain of USA was recently reviewed by Pritchett (1969) and Pritchett and Smith (1970). They concluded that many thousands of acres of forest could profitably be fertilized with N and P.

Deficiencies of these two nutrients have been found to limit conifer growth on a wide variety of soils in many countries. Phosphate fertilization is used as part of regular conifer forest management in New Zealand (Conway, 1962; Will, 1965; Mead, 1968), Australia (Gentle and Humphries, 1968), Great Britain (Binns and Grayson, 1967), and on the U S Lower Coastal Plain (Pritchett and Hanna, 1969). Most research and operational fertilization are with P at planting time, but good responses may also be obtained with old stands (Conway, 1962; Binns and Grayson, 1967; Mead, 1968; Pritchett, personal communication, 1971). Increased growth in older pine stands may be obtained for rates up to 200 kg/ha. Even at low rates (50 kg P/ha) growth stimulation may be observed for at least 10 years (Mead, 1968).

Nitrogen fertilization is a common management practice in older Scots pine (Pinus sylvestris L.) and Norway spruce

(Picea abies L.) stands in Scandanavia and in Douglas fir (Pseudotsuga menziesii (Mirb.) Franco) in the Pacific Northwest of the United States (Hagner)[1]. Extensive experiments in these northern latitudes suggest good responses to applications of 100 to 150 kg N/ha for Scots pine and spruce (Viro, 1965; Hagner, 1967; Brantseg, Brekka, and Braastad, 1970). In Douglas fir the optimum is somewhere between 200 and 400 kg N/ha (Gessel, 1968; Gessel, Stoate, and Turnbull, 1969).

There have been several reports of N increasing the growth of slash pine (Pinus elliottii Englem. var elliottii) stands past canopy closure. Jackson and Cloud (1958) reported improved growth in a stand fertilized with 14.5 kg N/ha as ammonium nitrate. In two experiments on moderately well-drained, loamy sands, Malac (1968) obtained response in 20-year-old slash pine to 370 kg/ha of mixed fertilizer (14-7-7) and to 52 kg N/ha applied as ammonium nitrate. Response was greater with the mixed fertilizer even though the same amount of N was applied. Broerman (1967) tested N and P in a factorial design, over a range of stand densities, in 15-year-old slash pine growing on moderately to poorly drained flatwood soil. The only significant growth response was to N and this was strongly modified by stand density. Walker and Youngberg (1962) reported that a 9-year-old slash pine plantation on a deep sand responded to 176 kg N/ha as ammonium nitrate, but not to 39 kg P/ha when the latter was applied either alone or in combination with N. Recent experiments

(Pritchett, personal communication) with older slash pine plantations on various soil types of the Lower Coastal Plain sometimes resulted in good responses to N and P. A positive N x P interaction also was noted in some tests.

High rates of N fertilization in older Scots pine or Norway spruce stands usually resulted in growth responses lasting 5 to 7 years (Viro, 1965; Hagner, 1967). With Douglas fir the duration of the N response has not been clearly established, although some experimental plots indicated increased growth from one N application through a 10-year period (Gessel, 1968).

Growth response to N applied to seedlings has been variable. When applied alone to slash pine, N has sometimes depressed growth (Merrifield and Foil, 1967), but when applied along with P it often has been beneficial (Bengtson, 1968; Brendemuehl, 1968; Pritchett and Smith, 1970; Pritchett, 1969). Interactions between N and P have been observed in other tree species (Richards, 1961; Brendemuehl, 1968; Richards and Bevege, 1969). The subject of N x P interactions was recently discussed by Bengtson and Holstener-Jørgensen (1971).[2] Causes for such interactions are poorly understood, but are thought to arise from soil-fertilizer reactions, plant-soil-microorganism relationships, and physiological factors within the plant.

Soil-Fertilizer Reactions

General

The reactions of N and P fertilizer materials with soil have been discussed in detail elsewhere (e.g., Bartholomew and Clark, 1965; Tisdale and Nelson, 1966; Black, 1968). This review will be confined to fertilizers used in this research project, namely ammonium-N and mono-calcium phosphate, and their reactions in typical Quartzipsamments.

Some of the typical forest soils of the Lower Coastal Plain were described by Pritchett and Smith (1970), and chemical and physical properties of virgin soils were given by Gammon et al. (1953). Generally, the soils are sands or fine sands of variable drainage characteristics. Total N in the surface of the moderately well-drained soils ranges from 0.04 to 0.15 percent and the carbon to N ratios from 18 to 15. The cation exchange capacity (CEC) varies from 2 to 10 meq; pH ranges between 4.0 and 5.5; and total P levels are about 100 ppm.

Reactions and Losses of Ammonium-N

The application of ammonium fertilizers to the soil surface may sometimes lead to volatile loss of ammonia or other gaseous forms of N. However, Volk (1959, 1961, 1970), working with Florida sandy soils, has shown that ammonia losses were negligible when ammonium salts were applied to bare, moist, acid soils, and unlimed grass sod (< 1 percent),

or when urea was applied to recently burned or unburned litter under slash pine forest (< 10 percent). Similar results were obtained by Overrein (1969) in a lysimeter study comparing N losses from urea, ammonium chloride, and potassium nitrate in a Scandanavian podzolic forest soil.

Gaseous loss, as nitrogen or oxides of nitrogen (denitrification), was reviewed by Broadbent and Clark (1965) and Bremner and Nelson (1968). Gerretsen and de Hoop (1957) obtained high losses (e.g., 30 percent) when ammonium sulphate was applied to acid, unlimed sands. It was suggested that at low pH, nitrites were formed more rapidly than their oxidization to nitrates. Nitrous acid is unstable below pH 5.5 and may decompose, or alternatively it may react with organic matter which would also lead to decomposition (Bremner and Nelson, 1968). The soils used by Gerretsen and de Hoop (1957), where gaseous loss was high, contained some nitrates which indicated that nitrification was normal. Most forest soils of the Lower Coastal Plain have little capacity for nitrification following additions of ammonium sulphate, unless they are limed (Eno and Blue, 1957; Maftoun and Pritchett, 1970). Overrein (1969) was unable to detect denitrification in a Scandanavian forest soil. According to Vlassak (1970) the incubation of forest soils (including sands from under conifer forests) results primarily in ammonification.

The addition of ammonium fertilizer to acid forest litter resulted in retention of some NH_4^+ on the cation exchange positions of the organic material. Biochemical reactions

were relatively rapid, whereby some NH_4^+ became non-exchangeable (Overrein, 1967a, 1970; Husser, 1971). The amount of non-biochemical fixation was quite small so that most of the N was readily available to plants (Jung, 1961; Overrein, 1967a; Husser, 1971). The additional N often resulted in increased biological activity and hence increased mineralization. Thus, under suitable environmental conditions, ammonium-N has been shown to exert a stimulating effect on humus-N release (Broadbent, 1965; Overrein, 1967b). Similar reactions appeared to occur with the organic matter of acid sandy soils (Jansson, 1956).

Leaching losses of N from ammonium salts are possible under some conditions (Volk, 1961; Cole and Gessel, 1965; Overrein, 1969; Jung and Dressel, 1970; Fiedler and Weetman, 1971[3]). Movement is usually greater than for urea, but less than for nitrates. The degree of movement is greatest in acid soils of low base saturation and where high rates of fertilizer are applied (Volk, 1961; Overrein, 1969; Fiedler and Weetman, 1971[3]). Leaching of ammonium also increased with addition of other salts (Volk, 1955).

In a field lysimeter study on a Scandanavian podzolic forest soil, Overrein (1969) reported the total amount of N leached over a 12-week period was equivalent to 40 percent of the ammonium chloride applied. However, not all of this leached N came from the fertilizer itself. Cole and Gessel (1965) found that 88 percent of N added as ammonium sulphate passed through the forest floor during a period of heavy rainfall.

The clay minerals found in the principal forest soils of the Lower Coastal Plain vary considerably (Fiskell and McCaleb, 1953). The sandier soils are often dominated by kaolinite or quartz, which together with their low clay content preclude fixation of large quantities of ammonium in clay lattices.

Reactions and Movement of Phosphate

The behavior of mono-calcium phosphate applied to soils was described by Fiskell (1965), Tisdale and Nelson (1966), and Huffman (1968). Water vapor moves rapidly into the granules and forms an extremely acid (pH 1.8), saturated solution. This diffuses out and reacts with soil constituents. In acid soils iron (Fe), aluminum (Al), and manganese (Mn) are formed. No reference was found indicating how this saturated acid solution reacts with litter on the forest floor or organic matter in the soil.

The absorption and movement of P in acid forest soils of Florida was investigated by Humphries and Pritchett (1971). In soils with low P sorption (i.e., Pomello, Leon, and Myakka), very little residual P from superphosphate applications 7- to 10-years previously could be detected in the top 20 cm. In the Kershaw and Rutledge soils, where P sorption was higher, the P was retained in a form that should be available to plants. The availability of this sorbed P declined with time. In a Bladen soil, which had high P sorption and buffering capacity, no movement of P was detected and the

decline in P availability had been more rapid than in the other soils. Data from a pot trial with these same soils corroborated these results (Mead and Pritchett, 1971). At the end of 8 months most of the applied P was readily available in the Myakka, Leon, and Pomello soils as indicated by foliage concentration, seedling uptake, and ammonium acetate (pH 4.8) extractable P. Availability of P was lower in the Kershaw and Rutledge soils and lowest in the Bladen soil.

White and Pritchett (1970), in sampling slash pine 5 years after fertilizing with surface-applied diammonium phosphate, found less than 1/9 of the residual P in the top 20 cm of soil. The soil was a Leon fine sand with low P retention capacity.

Ozanne (1962) studied phosphate leaching in a virgin siliceous sand in Australia. Over 50 percent of the applied superphosphate (20 kg P/ha) had leached to a depth greater than 1 m after 38 days. Rainfall during this period was 230 mm. Ozanne found indications that organic matter in these soils influenced P retention.

Riekerk and Gessel (1965) and Riekerk (1971) described the movement of P from the forest floor under Douglas fir using tagged solutions sprayed onto the litter. Leachate collected by tension lysimeter indicated that a pronounced flushing occurred immediately after the first rains. They estimated that 20 percent of the labelled P leached through the soil in the first year. The annual mobility of labelled P was about five times that of the native P, indicating a

difference between the more mobile ionic labelled fraction in contrast to the mainly organic native fraction. There were also indications of additional pathways of downward movement besides leaching, which probably included particulate matter transfer by suspension and by soil fauna. In interpreting these results it should be noted that the isotopes were added in a buffered nutrient solution, not as a regular fertilizer. The amount of P added was not given.

Uptake of N and P by Trees

Mycorrhizae

The importance of ectomycorrhizae in P uptake by conifers has been demonstrated many times (Morrison, 1962; Bowen, 1966; Hacskaylo and Vozzo, 1967; Mejstrik, 1970). Some evidence suggested mycorrhizae were also involved in N uptake (Hatch, 1937; Melin and Nilsson, 1952, 1953). Reasons for improved uptake by mycorrhizal plants are reviewed elsewhere (Harley, 1969, 1970; Bjorkman, 1970).

Tracer studies of phosphate uptake by beech (Fagus sylvatica L.) mycorrhiza in dilute solutions ($< 3 \times 10^{-4}$m) showed that the first labelled P compound in the host was inorganic phosphate and that its uptake with respect to time was linear (Harley and Loughman,1963). Thus,during initial absorption the phosphate passing into the host was not a result of mobilization of the phosphate in fungal tissue. However, this phosphate comprised only about 10 percent of initial P absorbed by the mycorrhizal organ as a whole; the remainder was localized in the fungal sheath (Harley and McCready, 1952). The P in the sheath was available to the plant at a more controlled rate (Morrison, 1957, 1962). About 50 percent of the phosphate taken up by the fungus was soon esterified (Harley and Loughman, 1963; Jennings, 1964).

Morrison (1962) compared the uptake of P by mycorrhizal and non-mycorrhizal pine seedlings grown under a variety of P nutrient conditions. He found that for periods up to 80

days, P accumulation in the tops was linear with time for mycorrhizal seedlings, but was distinctly non-linear for non-mycorrhizal plants.

The incorporation of ammonium-N in mycorrhizae has been studied for beech (Carrodus, 1967). His results showed that ammonium-N was initially absorbed by the fungal sheath. Absorption was related to synthesis of glutamine in the fungus.

Nitrogen Incorporation in Trees

In pines and many other plants, most N in the xylem sap is in organic compounds (Bollard, 1957; Barnes, 1962, 1963; Carter and Larsen, 1965). The most abundant amino-acid in pines is glutamine. The incorporation of inorganic-N into organic compounds occurs in the roots (Bollard, 1957; Barnes, 1962; Hill-Cottingham and Bollard, 1965; Hill-Cottingham, 1968). Barnes (1962) agreed with the hypothesis of others, that organic acids (e.g., α-ketoglutarate) serve as N acceptors and that on combination with N from the soil give rise to translocation forms of N (e.g., glutamine). Hill-Cottingham and Bollard (1965) believes their experiments with spring and summer N fertilization of apple indicated that all N reaching the crown was derived from reserve materials in the root and that N absorbed from the soil usually passed through a transitory storage phase. Fertilization accelerated mobilization of these storage materials.

Movement Within the Tree

Translocation in plants has been reviewed by Brouwer (1965) and Milthorpe and Moorby (1969). It is generally agreed that movement of N and P from the roots to the crown is in the xylem tissue and its subsequent retranslocation is mainly in the phloem.

Movement in the xylem is influenced by transpiration and metabolic demand (Biddulph, 1959; Laites, 1969; Milthorpe and Moorby, 1969). Transpiration is often the dominant mechanism, especially in long distance transport. Under conditions of low transpiration, metabolic demand may be the dominant factor controlling movement (Graham, 1957; Aibe, 1968). Biddulph (1959) and Steward and Sutcliffe (1959) suggested that internal factors may operate to determine if minerals in the transpiration stream will be shunted into local areas of accumulation as well as to control subsequent movement from one organ to another. Movement was greatest to leaves which were at the height of their expansion (Steward and Sutcliffe, 1959; Milthorpe and Moorby, 1969). Whereas most P going to very young leaves came from stored compounds, P accumulating in older and rapidly expanding leaves came largely from the roots.

Transpiration from trees varies with position in crown and shading, thus altering transport patterns within the shoot system (Kramer and Kozlowski, 1960). Stark (1969) reported that in Abies concolor Lind. transpiration was generally higher in the upper crown, in 'sun' needles, and in

very young foliage. By August transpiration rates had dropped in the upper crown and did not differ from the lower crown. In contrast Beysel (1960) found 1-year-old needles of Pinus nigra Arnold and Scots pine transpired at a lower rate than did 2- or 3-year-old needles.

Influence of Al on P Uptake and Translocation

The toxicity of Al to many plants has been well-established (Black, 1968). Aluminum ions cause inhibition of root growth through interference with cell division (Rios and Pearson, 1964; Riffaldi and Rotini, 1967). Sometimes the accumulation of high Al levels in roots was associated with reduced transport of P to the shoot (Wright and Donahue, 1953). This Al-P interaction may be due to precipitation of aluminum phosphates on the root surface or in the root cortex (Wallihan, 1948; Wright and Donahue, 1953; Clarkson, 1967). However, evidence is conflicting. Rasmussen (1969) noted that the patterns of accumulation of Al and P in cross sections of roots were very similar. He noted Al was excluded from the stele until lateral roots disrupted the endodermis. Clarkson (1967) indicated that the precipitating reactions occurred on the root surface and on the cell walls outside the cell membrane. He also proposed a second Al-P interaction inside the cell which influenced phosphorylation of hexose sugars. However, an x-ray microanalysis study of bean and barley roots suggested that the Al and P are not located in the same compartments (Waisel, Hoffen and

Eshel, 1970). Most of the Al accumulates in the protoplasts, not in the cell walls, and the distribution of P did not show special compartmentalization.

Several pine species were shown to have high Al foliage levels under some conditions (Black, 1968) which suggests they do not have an effective barrier at the roots. Humphries and Truman (1964) found the uptake of P and Al in the roots and shoots of Pinus radiata D. Don. were closely related.

Uptake Studies of P into Trees

The pattern of movement of P into tree crowns is poorly understood. Farrar (1953) introduced a root tip of a 4-year-old red pine (Pinus resinosa Ait.) into moist soil labelled with ^{32}P. He found detectable radioactivity in the crown after 40 hours. Activity increased for 2 weeks and then remained steady. One-year-old needles had higher activity than 2-year-old foliage. Tamm (1955) also found higher activity of ^{32}P in current needles of Norway Spruce. In an experiment with healthy and pole-blighted white pine (Pinus strobus L.) Ferrel et al. (1960) injected ^{32}P into the trunk and followed movement into the crowns. Accumulations were greatest in the upper part of the healthy trees and in the lower part of the crown of diseased trees. They suggested that this distribution pattern was directly related to transpiration rates.

Different patterns of ^{32}P uptake were observed by Walker (1958). Liquid, tagged phosphoric acid was applied in June

to the soil in a 3-year-old loblolly pine plantation. Needle samples were collected after 2, 8, 15, and 30 days from the upper, middle, and lower portions of the crown. On the second day activity was very high in the crown base, with much lower activities in the middle and upper crown. The high levels of activity in the lower crown decreased with time, although the lower crown consistently had more activity. One-year-old foliage contained more ^{32}P than the currently developing foliage at all sampling dates. Walker did not interpret his results.

Uptake Studies of Nitrogen into Trees

The uptake and distribution of ^{15}N in trees were studied by Nommik and co-workers. In one preliminary study Nommik (1966) applied ammonium sulphate, calcium nitrate, and calcium cyanamide to single tree plots in 11-year-old Scots pine on a podzolic sand. Fertilizer was applied in June and tissue samples collected at the end of each growing season (September or October) for three years. Uptake was greater for ammonium sulphate and calcium nitrate than for calcium cyanamide. At the end of the first growing season there was more ^{15}N in the new branch growth than in older branch portions. The level in the older branchwood was higher than in older needles; the level in the current branchwood was lower than in current needles. The level of ^{15}N had increased in the crown at the end of the second growing season, indicating additional uptake or translocation from the roots.

At this time ^{15}N levels were lower in the older foliage, but foliage levels were consistently higher than in the branchwood. At the end of the third growing season both needles and twigs showed a decline in ^{15}N atomic percent. In a second preliminary experiment with ^{15}N labelled ammonium sulphate applied to 12-year-old Norway spruce, similar results were obtained (Nommik, 1966). Levels of ^{15}N were lower in older foliage. At the end of two growing seasons trees of both these experiments were harvested. In the Scots pine 3 to 9 percent of the tagged material was recovered in above-ground parts. The corresponding figure for Norway spruce was 23 percent.

In another experiment Bjorkman, Lundeberg, and Nommik (1967) fertilized 15-year-old Scots pine growing on an iron podzolic soil. Labelled ammonium sulphate and calcium nitrate were applied at 60 kg N/ha in late May. Upper crown needle samples were collected at approximately 5-week intervals until late October, at which time the trees were harvested. Total N and ^{15}N increased with time, the greatest increase being in current needles. Trends were distinctly non-linear, with little increase in ^{15}N after 10 weeks. Both fertilizers produced very similar trends. At harvesting 7 percent of the applied N was in the above-ground parts of the trees, 2 to 18 percent was in ground vegetation and 9 to 12 percent was in the roots. Just under 60 percent was recovered from litter and soil, and,of the total amount of ^{15}N applied, 80 to 90 percent was recovered.

Nommik and Popovic (1967) compared the initial uptake of ^{15}N, ^{137}Cs, and ^{90}Sr by 11-year-old Scots pine to concentrations of total N, potassium (K), and calcium (Ca) in tissues. They found that total N in foliage, branchwood, and bark did not vary according to crown position, but new tissues had higher N concentrations than older tissues. Both total N and ^{15}N increased with time. After 2 months there were no large differences among ^{15}N levels in the various tissues.

The K concentrations did not differ with crown position but they were higher in older than in young needles. Activity of ^{137}Cs showed a clear increase in upper crown levels. Total Ca concentrations increased with tissue age and concentrations were greatest in the lower parts of the crown. Most ^{90}Sr activity also increased with tissue age. Thus, every isotope had a distinct pattern of uptake, and these were not necessarily related to tissue concentrations.

Isotopes and Nutrient Uptake Studies

The use of isotopes in tree nutrition research was discussed by Fraser (1956) and Walker (1958). Advantages included the direct measurement of transport velocities and the separation of newly arrived nutrient elements from that already present in various components of the ecosystem (Riekerk and Gessel, 1965).

Hauck (1968) reviewed the possibilities, problems, and assumptions in using ^{15}N as a tracer, with special reference to forest problems. A selected bibiligraphy of ^{15}N in

agricultural research was published by Hauck and Bystrom (1970).

The main disadvantages of isotopes in forest studies are their cost, and with radioisotopes, health hazards and the possibility of contaminating the environment (Hauck, 1968; Riekerk, 1971). Thus, most studies have used single tree plots (Walker, 1958; Nommik, 1966; Nommik and Popovic, 1967; Bjorkman, Lundeberg, and Nommik, 1967; Riekerk, 1971).

Seasonal Foliage Changes in Conifers

The changes in dry weight and N and P concentrations in foliage samples give valuable information on seasonal patterns of nutrient movements. Such studies are numerous with forest trees, although most have been related to developing tissue sampling procedures.

Dry weight of newly forming needles increases rapidly in the spring. A peak may be reached in early winter, after which a decline is observed (Lowry and Avard, 1969), or dry weight may continue to increase slowly during the winter (Wells and Metz, 1963). Dry weight increases rapidly again the following spring reaching a peak in summer. A second decline may follow this peak. Dry weight losses indicate utilization *in situ*, translocation or leaching losses (Lowry and Avard, 1969).

New needles show high N concentrations soon after flushing but decline rapidly. The level drops to a minimum in mid-summer and rises again to another peak in autumn (September). This is followed by a gradual decline until needle fall (White, 1954; Tamm, 1955; Wells and Metz, 1963; Lowry and Avard, 1969; Smith, Switzer, and Nelson, 1970). These patterns were similar in various levels of the crown although different in magnitude. Concentrations of N are usually higher in the upper crown than in the lower crown (White, 1954; Lowry and Avard, 1965; Smith, Switzer, and Nelson, 1970). However, Wells and Metz (1963) reported that the upper crown of loblolly pine had lower concentrations, and Nommik and

Popovic (1967) did not find differences among crown levels in Scots pine.

The seasonal pattern for P concentration in foliage may show similar trends to that of N (Tamm, 1955; Lowry and Avard, 1969). White (1954) and Wells and Metz (1963) did not find a rise in P concentration in the autumn, but rather a slow consistent decline until the needles were a year old.

Several studies indicated that upper crown foliage has slightly higher P concentrations (White, 1954; Wright and Will, 1958; Wells and Metz, 1963). Other studies reported no differences (Humphries and Kelly, 1962; Lowry and Avard, 1965). Most show that current needles have higher P levels than older needles.

Biomass and Nutrient Cycling in Pine Forests

Techniques used in biomass studies were described by Rennie (1966), Ovington, Forrest,and Armstrong (1967), Madgwick (1971), and White and Pritchett (1970). A summary of forest biomass data was given by Art and Marks (1971). Nutrient cycling in forests was reviewed by Weetman (1961), Ovington (1962) and Curlin (1970). Bray and Gorham (1964) summarized litter production in forests and Tukey (1970) reviewed foliar leaching.

The most complete synthesis of biomass accumulation and cycling in Southern pine was made by Switzer, Nelson and Smith (1966, 1968) and Switzer and Nelson (1970)[4]. Their data showed foliage biomass of loblolly pine reached a maximum of 3000 to 4000 kg/ha at age 25. Branchwood and stemwood had a later maximum; about 40 years. At age 20, branchwood amounted to 8,000 kg/ha and stemwood was 60,000 kg/ha. Current annual increments for foliage, branchwood, and stemwood reached a maximum between ages 20 to 30 years. During the first 20 years total ecosystem biomass increased from 10,000 kg/ha to 105,000 kg/ha. Herbaceous vegetation declined rapidly in the first 7 years. Litter accumulation stabilized at about 16,000 kg/ha around age 15. Accompanying biomass changes were similar changes in nutrient contents. Total N in the undergrowth dropped in the first 7 years from 75 kg/ha to near zero. Foliage N content rose rapidly and reached a maximum at age 20 of about 60 kg/ha. At 20 years there were another 173 kg N/ha in other parts of the tree and

120 kg/ha in the litter. Similar changes occurred with P. By the 20th year the forest floor had 9.1 kg/ha of P.

The proportion of the total N and P in the above-ground part of the system that was cycled in the 20th year was 23 and 19 percent respectively. Of the total requirements at this age 84 and 93 percent of the N and P came from cycling process. The major external source that made up the 20-year requirement was rainfall, not the soil. Of the amount of N being cycled, 46 percent was in internal cycles, 48 percent was in litter fall and decomposition and 6 percent was in rainwash. With P the internal cycle accounted for 60 percent of the total quantity cycling and litter fall and decomposition accounted for 25 percent. Rainwash contributed 10 percent to the P cycling. Of the total annual requirements, 86 and 90 percent of the N and P went into foliage production.

Will (1968) has studied nutrient requirement of Pinus radiata D. Don. on good sites. He estimated that after the first 10 years the net annual demand from the soil would be about 0.25 kg/ha for P and zero for N. These estimates agree well with the work described above.

Nelson, Switzer, and Smith (1970) investigated the accumulation of nutrients in loblolly pine between the 4th and 5th year after planting. The net increase in N and P was 34.2 and 4.7 kg/ha,respectively and a large proportion of this went into foliage production. The seasonal pattern of N uptake followed that of dry matter, with some 20 percent of the

N being accumulated during the cool season (October-February). Accumulation of P was more rapid. The whole of the year's uptake occurred before September, and there was a loss of P during winter. The pattern of N accumulation in bark, wood, foliage, and apical growth revealed that much of the N was translocated out of the wood and bark and used by the developing foliage. The accumulation of N in the bark and wood took place before needle flush and again in the late summer.

Summary

There are good prospects that N and P fertilizers will be used on some older pine stands of the Southern Lower Coastal Plain. However, little is known as to the fate of these nutrients when applied under these conditions.

A relatively small portion of N from ammonium fertilizers is probably held in the litter layer. It can be expected to move through the mineral soil, but to an unknown degree. A large portion of the added N in the litter and soil will become immobilized by microorganisms, although over a long time period this should become available to the plants. Nitrification or denitrification in these soils is probably of little importance.

Ammonium-N is taken up rapidly by mycorrhizal pine roots and assimulated into organic-N compounds. Nitrogen compounds are translocated in the xylem to the tree crowns and should accumulate in regions of high transpiration and/or high metabolic activity. Over several growing seasons the nitrogen will become more evenly distributed through further uptake, internal redistribution, and nutrient cycling processes.

Monocalcium phosphate can also be expected to move through the litter layer into the top soil. On some soils it then undergoes rapid fixation but in certain soils it is subject to leaching. Uptake of P should be linear with time over the first few weeks after fertilizer applications, when it is applied at the start of the growing season. The initial

distribution in the crowns will probably be related to transpiration and metabolic demand. This pattern may possibly be modified by Al-P relationships within the plant. Results of ^{32}P uptake studies and on transpiration measurements in trees have been inconsistent.

Nutrient cycling is an extremely important factor in tree nutrition. Some 80 to 90 percent of the N and P needed for the formation of new tissue is from cycled nutrients. About 45 percent of the cycle is within the tree itself.

Fertilization results in an increased pool of nutrients being cycled, and furthermore can influence tree growth for many years. A knowledge of nutrient cycling and nutrient movement is necessary for the proper use of fertilizers in forests.

NOTES

[1]Hagner, S. 1971. The present standard of practical forest fertilization in different parts of the world. Paper presented before Sec. 32, XV IUFRO Congress, Gainesville, Fla. 16 p.

[2]Bengston, G. W. and H. Holstener-Jørgensen. Interactions of nitrogen and phosphorus: their effects on forest tree response to N-P fertilization and on the diagnostic value of foliar analyses. Paper presented before Sec. 21, XV IUFRO Congress, Gainesville, Fla. 17 p.

[3]Fiedler, F. J. and G. F. Weetman. 1971. Losses of nitrogen from surface applied urea and other effects of season of fertilizer application on growth response. Paper presented before Sec. 21, XV IUFRO Congress, Gainesville, Fla. 25 p.

[4]Switzer, G. L. and L. F. Nelson. 1970. Nutrient accumulation and cycling in loblolly pine (Pinus taeda L.) plantation ecosystems: The first twenty years. Paper presented before Div S-7, Soil Sci. Soc. Amer. Meetings, Tucson, Ariz.

MATERIALS AND METHODS

Experimental Site

The experimental area is situated in compartment eight, Austin Cary Forest. This forest is owned by the University of Florida and lies about 15 km northeast of Gainesville in Alachua County, Florida.

Evidence from old buried stumps and local history indicated that the area once supported longleaf pine (Pinus palustris Mill.) forest. Little is known about the use of the area between the time the forest was felled and the area was purchased by the University, except that once it was under cultivation.

The area was burned and hand planted to slash pine in December 1957-January 1958. The seedlings, which orginiated from seed collected from a single, open-pollinated seed source, were planted at 1.8 x 3.0 m spacing.

An N, P, K composite factorial fertilizer trial was established in the area in June 1958 (W.L. Pritchett, personal communication). The fertilizer treatments (0, 29, 50, 71,and 100 g of N, P_2O_5; or K_2O) were applied to an area of 0.6 m radius around the seedlings. Treatments were reapplied in April 1962. Negligible growth response was observed, the main effect of the fertilizers being to decrease survival.

It is not surprising that the trees did not respond to fertilization, for measurements made in April 1969 indicated the area was of site quality 75-80 (Barnes, 1955). In 1969 the stand was 11 years old and the trees had a mean height of 12.1 m and mean diameter at breast height (dbh) of 14.2 cm. There were 1,547 stems/ha and 25.0 m^2 of basal area. About 20 percent of the trees were severely suppressed having dbh's of $\leq$ 5 cm.

The canopy of the unthinned stands was tight and the tree crowns narrow. There was a well-developed litter layer of 3 to 4 cm thick. The light ground vegetation was dominated by Rubus sp and grasses, with occasional Carex sp, herbs and shrubs.

The trees had a high incidence of Cronartium fusiforme, a disease which produces severe malformation in slash pine.

The climate of the area can be broadly classified as sub-tropical. The mean annual temperature for the region is 21.1°C with three months, December, January, and February, where the average monthly temperature falls below 15°C (U.S. Weather Bureau, 1970). The hottest months of the year are May through September when the temperatures average 25 to 30°C. Mean annual soil temperature is 23°C and mean annual rainfall is 1330 mm. Rainfall is unevenly distributed with almost half falling during the four summer months, June through September. The driest period is from November to January when average monthly rainfall is less than 75 mm.

Rainfall data from mid-July 1968 to February 1971 at the

University of Florida, Beef Research Unit are given in Figure 1. The distance between this raingauge and the experimental site is less than 4.5 km.

The soil is moderately well-drained and classified as a member of the siliceous, hyperthermic, uncoated family of Typic Quartzipsamments. It was formerly mapped as a low phase of Blanton (W.L. Pritchett, personal communication). Under the recently adopted soil classification scheme in the United States (Soil Survey Staff,1970a, 1970b) it closely resembles the Tavares series, but differs by having a thicker A_1 horizon.

The soil has 2 to 4 cm thick litter (A_0) over an A_1 of 40 to 50 cm (Appendix A, Table 25). The A_2 is between 50 and 150 cm thick and is white or light grey with occasional mottles. A dark, sometimes indurated,B_2h horizon occurs between 1 and 2 m.

The topsoil (A_1) is sandy with a silt plus clay fraction of 5 to 9 percent. Bulk density increases with depth. The soil is acid,and by agricultural standards, has a low C.E.C., organic matter content,and available nutrients (Table 1 and Appendix A, Table 26).

The upper part of the A_2 has less fine material than the A_1 horizon, but fines increase again with depth (Appendix A, Table 26). Bulk density is higher in the A_2 than in the A_1.

The watertable fluctuates greatly. At the time of root excavation, during the dry season, it was at 2.25 m depth. During the wet season it is much closer to the surface (<0.5 m).

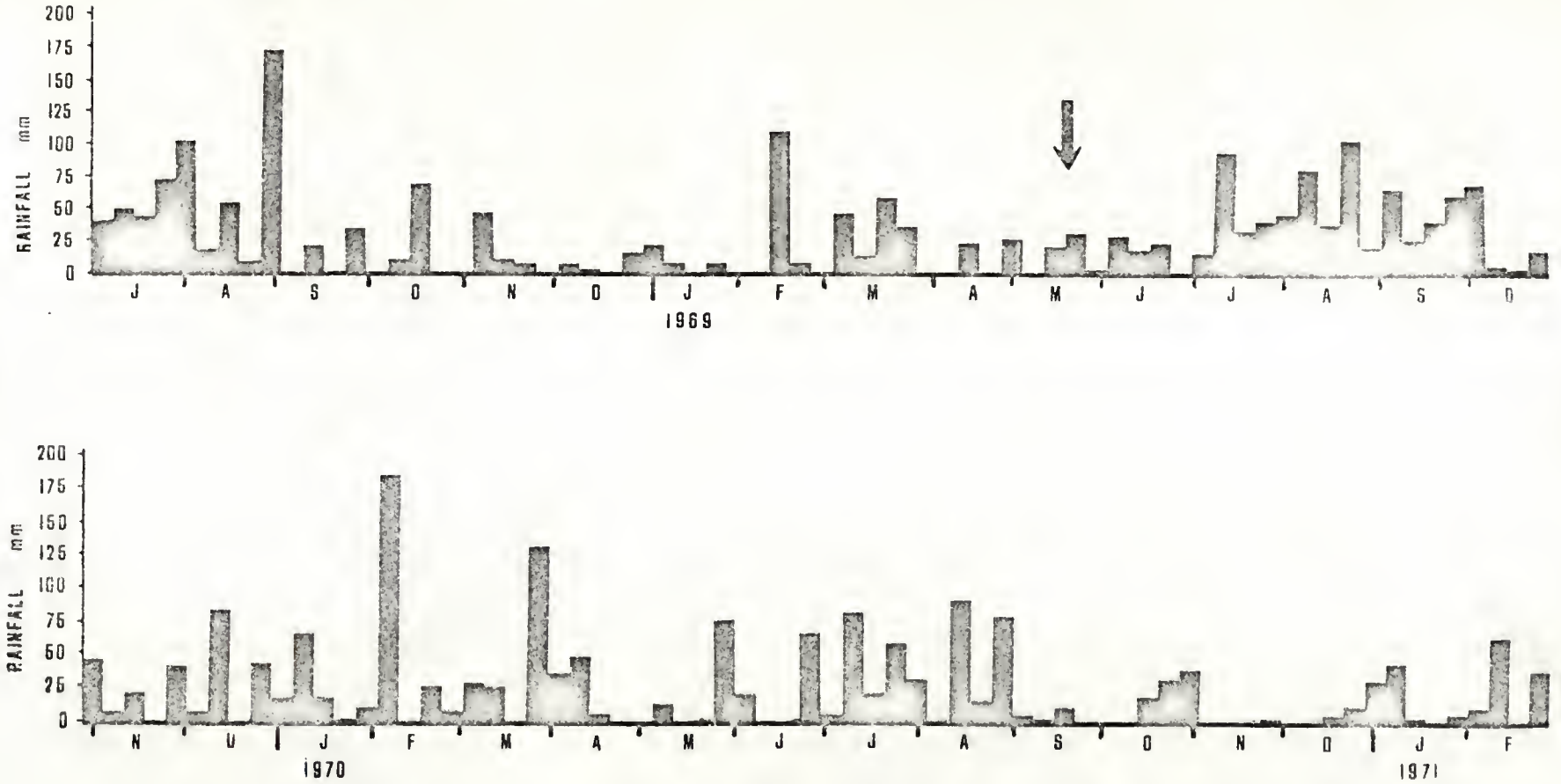

Figure 1. Precipitation at the University of Florida, Beef Research Unit between July 1968 and February 1971. Arrow denotes time when fertilizer applied.

Table 1. Summary of physical and chemical properties of untreated topsoil at the experimental site, Austin Cary Forest.

Depth	Total sand	Silt	Clay	OM[a]	Bulk density	pH[b]	CEC	Total[c] N	Total[c] P	Available[d] P	Available[d] K	Available[d] Ca	Available[d] Mg	Available[d] Al
	%				g/cm^3		meq/100g	%	ppm	ppm				
0-10	91.8	5.5	2.7	1.72	1.32	5.0	3.52	0.042	135	1.06	9.2	15	2.5	45
10-20	91.8	5.1	3.1	1.36	1.47	5.2	2.82	0.030	109	1.03	6.4	tr	2.5	73
20-30	92.7	3.9	3.4	1.28	1.52	5.3	2.49	0.027	90	0.72	4.4	tr	2.5	116
30-50	92.7	3.9	3.5	0.87	1.56	5.3	1.94	0.022	82	0.57	3.8	tr	2.5	127

[a] OM = organic matter.

[b] pH of soils before fertilization using a 1:2 soil-water suspension.

[c] Total N by salysilic acid modification of Kjeldahl procedure.
Total P by sodium-carbonate fusion.

[d] NH_4OA_c (pH 4.8) extractable - mean of all plots.

Experimental Techniques

General

In order to achieve the defined objectives, tracer techniques using labelled fertilizers were employed. They provide sensitive methods of following movement of applied nutrients to various parts of the ecosystem.

The study can be divided into the following sections:

1. The initial uptake of N and P by the trees. This was followed for 10 weeks.

2. The longer-term changes of N and P in the tree crowns as influenced by fertilizer rate, seasons, and foliage age. These changes were followed for two growing seasons.

3. The movement of N through the litter and in the soil profile. This was studied over 19 months.

4. The distribution of labelled N in the ecosystem at the end of the second growing season.

5. Supplementary studies.

Experimental Design

A completely randomized design, with four replications of three treatments,was employed. Each plot consisted of a single, codominant tree. The treatments applied were:

1. No N
2. 56 kg N/ha
3. 224 kg N/ha

The N was applied as granular ammonium suphate labelled

with ^{15}N (Table 2). A basal dressing of 90 kg P/ha as granular, concentrated superphosphate (CSP) was applied to all plots. Two trees in treatment three were fertilized with ^{32}P labelled CSP so that initial movement into their crowns could be followed.

All fertilizers were prepared and provided by the Tennessee Valley Authority, National Fertilizer Development Center, Muscle Shoals, Alabama.

Tree Selection and Fertilization

The 12 trees were selected so that between-tree-variability was at a minimum. All trees were in the Tavares soil type; were codominants of similar heights and diameters; had similar crown characteristics with regard to number of whorls (8 to 10) and multinodal branching habit; were in areas of light ground vegetation and well-developed litter layer. The trees were separated by more than 12 m to avoid the possibility of cross feeding. The selected trees ranged in dbh from 14.7 to 15.5 cm and in height from 12 to 13 m.

In order to produce similar competitive conditions for each tree and to reduce uptake by surrounding trees, trees within 3 m were felled. With trees planted at 1.8 m spacing in rows 3 m apart, this required the removal of either one or two trees around each sample tree.

An area of 1.5 m radius (7.07 m^2) was fertilized around each tree. Fertilizers were spread evenly on the undisturbed litter surface. One quadrant was fertilized at a time, the

Table 2. Fertilizer materials used in study of movement of N and P in a slash pine ecosystem.

Material	Mesh	Isotope
Concentrated superphosphate - 24.9%P	6 - 9	0.236 mc ^{32}P/gP
Concentrated superphosphate - 21.8%P	6 - 9	not labelled
Ammonium sulphate - 21.2%N	6 - 12	2.388 atomic % ^{15}N

amount of fertilizer for each quadrant having been weighed in the laboratory. All fertilizers were applied on the afternoon of 19 May 1969.

Initial Uptake

In two trees (numbers 9 and 10), the initial uptake of ^{32}P and ^{15}N and changes in N and P concentrations were followed for 71 days. These were selected randomly from the 12 sample trees before fertilization and received the high rate of N (224 kg N/ha as ammonium sulphate) and 15 mc ^{32}P as CSP.

Towers were constructed around the two trees to facilitate sampling (Figure 2). Their foundations were outside the fertilized area. Trampling and litter disturbance were minimal. Fences were used to keep the public away from the radioactive fertilizer and from climbing the towers (Figure 2).

For background levels of ^{15}N and radioactivity, samples of current (1969) needles and 1-year-old (1968) needles were collected from the upper-mid crown prior to fertilization. Subsequent foliage samples were taken 1, 3, 5, 7, 11, 15, 21, 28, 35, 42, 49, 56, and 71 days after fertilization. At each of these dates, samples were collected from three positions in the crown (terminal leader, upper crown, and lower crown) and from first- and second-order branches (Figure 3). On the first day and at alternate sampling dates, samples were collected for all needle ages. Two years of needles were present on the leader and upper crown first-order branches.

Figure 2. One of the two towers constructed around the sample trees used to follow initial uptake. These towers simplified the frequent collection of samples from several crown positions. Note fence and rain collector.
Photograph G.W. Bengtson.

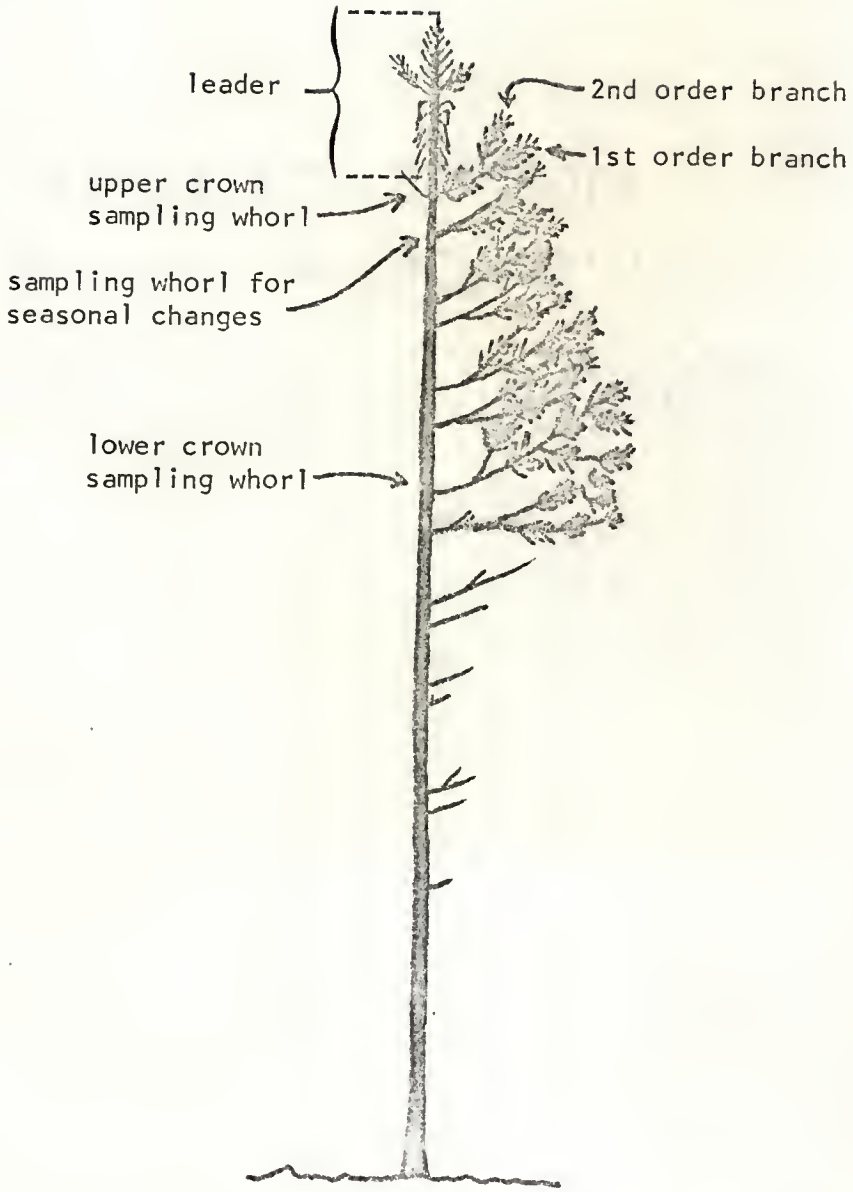

Figure 3. Sampling scheme for initial uptake studies. The position of the long-term sampling whorl is also shown - compare with Figure 4.

Only current foliage was present on the upper second-order branches because the upper whorl had been formed in the previous growing season.

A foliage sample consisted of a small number of fascicles collected from all branches in the whorl at a particular crown level. Thus, only a few needles (the terms needles and fascicles are used interchangeably from here on) were taken from a branch at any one sampling date in order to avoid severe foliage reduction. As needle development is acropetal, in relation to stem position, samples of current needles were taken from lower portions of the flush. All samples came from the main spring flush. A second smaller flush was observed later in the growing season, but this was not sampled.

Samples were dried at 60°C within a few hours of collection and ground in a Waring blender prior to analysis.

Long-Term Foliage Changes

The pattern of change in foliar P, Al, N, and ^{15}N concentrations, and in needle weight and length, were followed by sampling at 6-week intervals from May 1969 to December 1970. All twelve trees were sampled so that the effect of N treatment could be evaluated.

Foliage was collected from all second-order branches in a selected whorl. This marked whorl was in the upper crown at the beginning of the experiment, but because of tree

growth, it was in the low-mid crown region on later sampling dates (Figures 3 and 4). Samples were collected from the same branches during both growing seasons so that the trends could be followed in the same groups of needles.

All ages of foliage present were sampled, with sampling being restricted to the first flush for each year. In order to reduce damage to tree crowns by excessive defoliation, foliage was bulked by treatment in two out of three sampling dates.

Samples were placed in plastic bags and stored in the refrigerator if drying was delayed. A random selection of 25 needle fascicles was taken from each sample for measurement. Needles with dead tips were acceptable, but at least one needle/fascicle had to have an unbroken tip. The longest needle in a fascicle was measured to the nearest millimeter. After drying at 60°C the 25 selected fascicles were weighed to the nearest milligram. In some samples of old needles, 25 perfect needles were not available, so a smaller sample was used. Results were converted to weight per fascicle (needle weight) and weight per unit length of fascicle.

The number of needles per fascicle were recorded for 1969 and 1970 needles collected on 11 July 1970. The 1969 spring needle flush had started before fertilization so that a comparison of 1969 and 1970 needles at this date indicates the influence of treatment on this character.

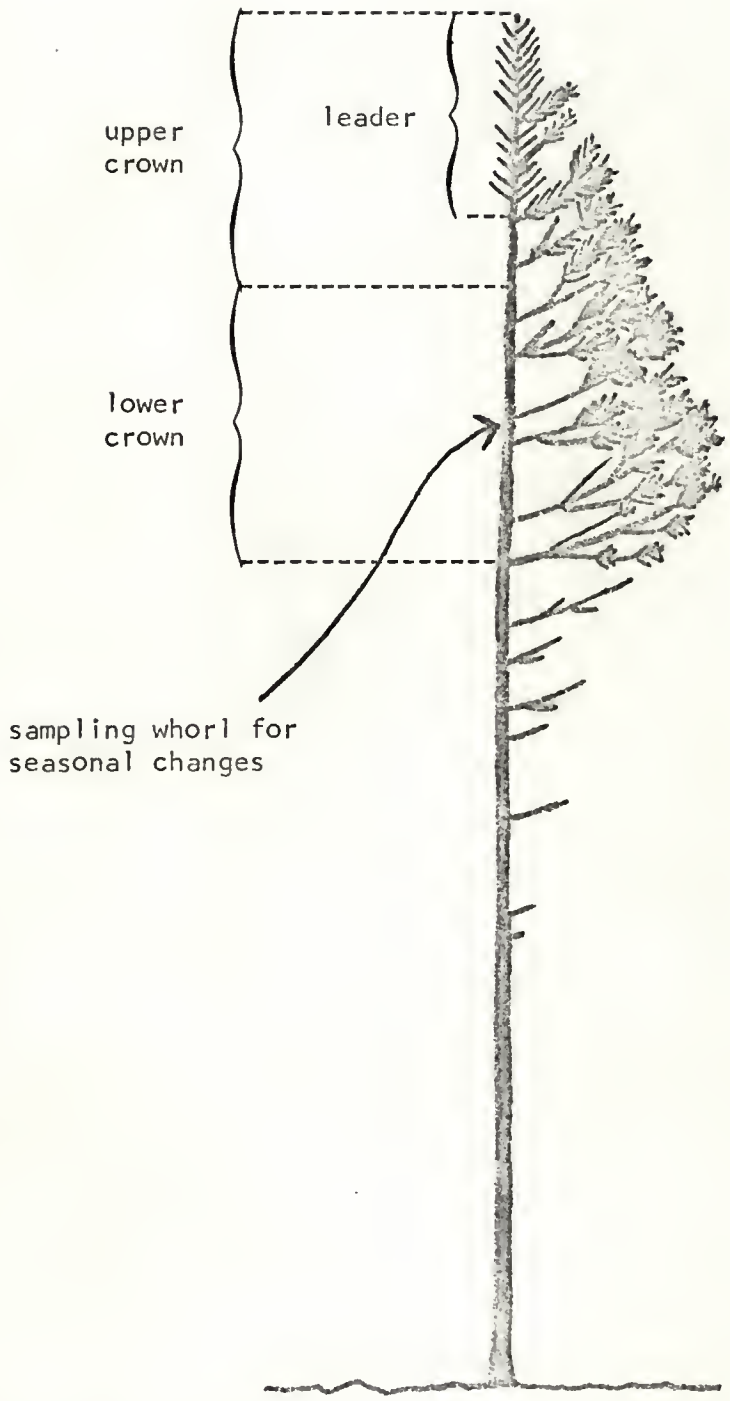

Figure 4. The subdivision of the crown at harvesting, which was two growing seasons after fertilizer application.

Sectional aluminum ladders were used to climb the trees. Biomass data on dead limbs will have little meaning, for many dead limbs along one side of the tree were broken by the ladders.

Movement of N in Soil

The movement of fertilizer N down the soil profile was followed by collecting samples at 0, 6, 12, 30, and 84 weeks and analysing for total N and ^{15}N. Samples were collected from the litter and in the A_1 horizon to a depth of 50 cm by 10-cm increments. Except for the final sampling date, samples were bulked by treatment. Six 2.5-cm diameter cores were collected per plot. Selected control samples were analysed to give the background level of ^{15}N in the soil.

Ecosystem Distribution of ^{15}N

The final destructive sampling was made in the winter of 1970-71. All components of the ecosystem were sampled and the amount of ^{15}N in each determined. The above-ground sampling of litter, ground vegetation, and trees was made from 14 to 24 December 1970. The roots were excavated during January 1971.

Tree stem

The following procedure was used to determine total dry weight in the stem and to subdivide this according to bark, recent wood, and old wood. Recent wood was defined as that formed during the last two growing seasons.

After delimbing the felled tree, the bole was taken to a nearby covered work area where it was sectioned into 1.3-m long bolts. The last 2 years of leader growth were treated as a separate unit, being divided into bark and recent wood and not being subsampled before drying. The other bolts were weighed green and subsampled by cutting two discs from their center. Knots were avoided. The discs were weighed to the nearest gram and one was subdivided into bark, recent wood, and old wood. All samples were dried at 60°C and reweighed. The second section, which was dried intact, was used to check for losses during removal of bark or recent wood.

The weight of bark, recent wood, and old wood in a bolt was calculated by proportioning the green bolt weight according to the fraction of dry component to green weight in the sample disc. The total weight of the components in the stem was found by addition.

Tree crowns

The live tree crown was divided into upper crown, lower crown, and terminal leader (Figure 4). Any branches originating on the stem above the mid-point of the crown were considered to be in the upper crown. Those below the mid-point were classified as in the lower crown.

Foliage was subdivided into these three crown classes and also by needle age. All foliage was removed, dried at 60°C in large paper bags and weighed to the nearest gram.

Branches were divided into five categories: dead and two age groups each in the upper and lower crown. Recent branches (i.e., age 1969-70) were the terminal portions formed in the last two growing seasons. Older branches (i.e., pre-1969) included those portions initiated prior to the 1969 growing season. Older branches were not always present in the upper crown. All branches were cut into sections, dried in paper bags at 60°C and weighed to the nearest gram.

The dormant buds were collected separately and were divided into two categories, upper crown (which included the leader bud) and lower crown. Buds were dried at 60°C and weighed to the nearest 0.1 g.

Tree roots

Roots were divided into the following categories:

1. stump
2. large taproots and sinkers
3. fine taproots (≤2.5 mm diameter)
4. inner large laterals
5. inner fine laterals (≤2.5 mm diameter)
6. outer large laterals
7. outer fine laterals (≤2.5 mm diameter)

Inner roots are those from within the fertilized area, i.e., within 1.5 m of the tree center. Outer roots are those extending beyond this area (Figure 5). All inner laterals and taproots were collected and their dry weight obtained.

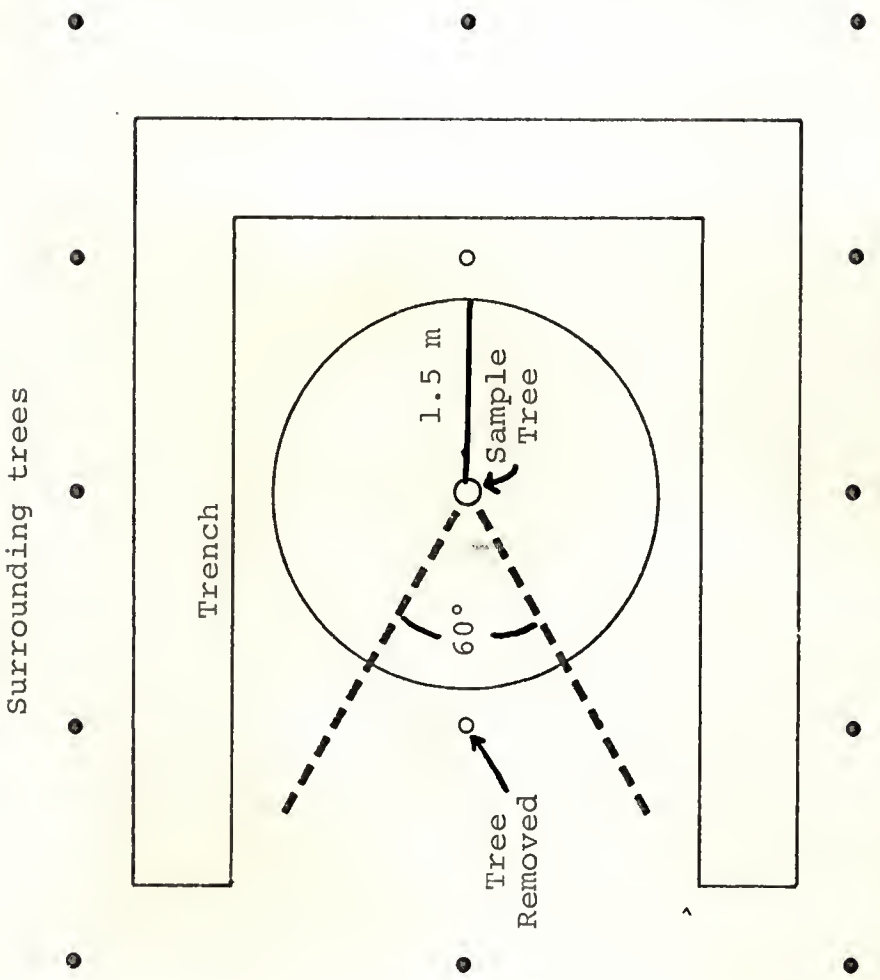

Figure 5. The plot layout, sampling scheme used during root excavation, and positions of surrounding and felled trees.

However, while all taproots were subdivided into fine and large roots, only those laterals from a 60° segment were subdivided (Figure 5). The total dry weight of inner laterals was proportioned into large and fine roots using the ratio found in this sample. Outer roots were collected from the 60° segment only (Figure 5). These were also subdivided into large and fine roots. The outer root dry weights were obtained using the weight relationship between inner and outer roots for the 60° segment and the total weight of inner roots. Roots were weighed to the nearest gram after drying at 60°C.

The first step in excavating the root systems was to dig a trench about 1.5 m deep and 0.6 m wide around three sides of the sample tree using a backhoe. The next step was to sluice one side of the trench to the stump using water supplied under pressure (Figure 6). This exposed the stump and taproots and enabled the laterals to be tagged and severed. The taproot was then removed by a combination of lifting and washing. Taproots were removed as early as possible in the excavation as these went down a depth of about 2 m and would have been difficult to remove once the trenches were filled with soil. With the taproot removed, laterals were carefully washed free one at a time. It was estimated that excavation of a single root system required 60 to 80 man-hours.

Ground vegetation and litter

Prior to tree harvesting, all live ground vegetation

Figure 6. The excavation of root system at a stage prior to removal of the taproot.

Photo R.E. Weiss

within 1.5 m and from 1.5 to 2.5 m of the trees was collected. Two litter samples of 1.0 m^2 area were collected from each plot; these samples were dried at 60°C. Ground vegetation was weighed to the nearest 0.1 g and the litter samples to the nearest gram.

Dry weight of surrounding trees

To account for ^{15}N taken up by surrounding trees it was necessary to estimate their dry weight as well as to sample them. The estimate of dry weight was obtained by measuring the dbh of the surrounding trees and determining the relationship between this parameter and dry weight. An extra five trees were felled so that, along with the 12 sample trees, they covered the range of diameters within the stand. The dry weights of foliage, branches, and stems of these trees were obtained.

The relationship between dbh and dry weight took the form:

$$\log \text{dry weight} = a + b \log \text{dbh}.$$

A foliage sample was collected from each tree immediately adjacent to a plot fertilized with tagged N. These samples were collected from all parts of the crowns and included all ages of foliage.

Soil samples

Soil samples were taken from all plots during root excavation. Sampling was to a depth of 2 m by 10-cm increments.

Subsequent bulking was performed on the basis of equal dry weights.

Bulk density samples were collected using a double cylinder, hammer-driven core sampler which gave a sample 7.5 cm long by 7.5 cm diameter. Samples were collected from all plots to a depth of 50 cm. In one plot (number 10) bulk density samples were also collected at 20-cm intervals between 50 cm and 200 cm.

Supplementary Studies

Rainfall information

Rainfall reaching the forest floor was recorded during the 10 weeks following fertilization. Five sample collectors of 20 cm diameter were placed under the trees.

Other rainfall data were obtained from the University of Florida, Beef Research Unit.

Growth data

The height, diameter, and volume increments of the sample trees, between the time they were fertilized and harvested, were determined by stem analysis. Total height at felling and height in the winter of 1968-69 were measured to the nearest centimeter. Overbark diameters, underbark diameters and the diameters in the winter of 1968-69 were measured to the nearest millimeter at the base of the tree and at 1.3 m intervals up the stem. Overbark diameters were measured with a diameter tape and underbark diameters were obtained by averaging two

cross-sectional measurements. Volumes were calculated using Smalian's formula, the leader being treated as a cone.

Height to green crown and the height to the long-term sampling whorl were also measured at harvesting. Shortly before felling three measurements of crown radius were obtained using a vertical line finder. 'Crown area' was calculated as the area of the curved surface of a cone with height equal to crown length and basal radius equal to crown radius. Crown area was used along with pretreatment stem measurements in a covariate analysis of response.

Influence of fertilizer on pH

Soil samples collected before treatment and at 6, 30, and 84 weeks were all analysed to determine the influence of fertilizer on pH. Data were analysed as a split-split-plot with fertilizers as main plots, and time and soil depths as the sub- and sub-sub- plots, respectively.

Sample Analyses

Preparation of samples for analysis

Litter, foliage, ground vegetation, wood, branches, and root samples were all ground through a 2-mm screen. Bark and bud samples were ground through 1-mm and 20-mesh screens respectively. Litter and foliage samples were subsampled after grinding using a sample splitter. The foliage sub-sample was then reground through a 1-mm screen. Regrinding was not necessary for litter as it powdered on grinding. The

terminal leader, branches, stump, and coarse roots were subsampled before grinding by slicing discs at about 10-cm intervals using a band saw. The samples of old wood also had to be sliced before grinding. Wood, branch, and root samples were not reground through a finer screen because a large sample was necessary for chemical analysis.

Bark and wood samples, collected at 1.3-m intervals along the tree stem, were bulked so that there was a single sample each of bark, recent wood, and old wood for every tree. Bulking was made on the basis of the components dry weight in the bolt. The resulting samples were mixed well; a mechanical blender was used for larger samples.

Bulk samples were also made for the foliage collected from the surrounding trees. The estimated weight of foliage in the crown was used as a basis for mixing the dried ground samples.

Soil samples were air-dried, sieved through a 2-mm screen and stored in airtight bottles.

Chemical analysis

Soil pH was determined in a stirred 1:2 soil-water suspension, using a glass electrode; CEC by ammonium saturation using 1.0 N ammonium acetate at pH 7.0 (Chapman, 1965); organic matter by a modified Walkley-Black method (Jackson, 1958); and particle size distribution by the hydrometer method (Day, 1965), with the sand fractions being subdivided by sieving for 15 minutes through U.S. Standard sieves.

Extractable P, K, Ca, magnesium (Mg), and Al were determined in filtrates after shaking soil with N ammonium acetate buffered at pH 4.8 (1:5 soil-solution) for 30 minutes. Phosphorus was determined by ammonium molybdate - stannous chloride colormetric procedure (Jackson, 1958), K by flame spectrophotometer (Jackson, 1958), Mg, Al and Ca by atomic absorption spectrophotometer. Lanthanum oxide was added to suppress interferences in the Mg and Ca determinations (Breland, 1966).

On a few soil samples collected at the end of the field experiment, nitrate and nitrite were determined in a 1:5 soil - solution extracts by the phenoldisulfonic acid and sulfonilic acid, alpha - napthylamine procedures, respectively (Jackson, 1958). No nitrate or nitrite could be detected. Nitrates were also determined, by specific ion electrode, on all samples collected from the high-N plots prior to and following the fertilization. The procedure used was similar to that described by Meyers and Paul (1968). A 1:2 soil-water mixture was prepared, stirred occasionally for 30 minutes and the nitrate measured in the supernatant liquid. The supernatant liquid was stirred with a magnetic stirrer and care was taken to ensure equilibrium before the reading was recorded. An Orion specific ion electrode was used in conjunction with a model 801 Orion ionalyzer.

In order to check the reliability of the nitrate-ion electrode method in these soils where levels are very low, a series of soil samples were prepared and known quantities

(0, 3.1, and 6.2 ppm) of nitrate added. The experiment is described in detail in Appendix G.

As low levels (≤5 ppm) nitrate were detected, total N was determined by the salicylic acid modification of the Kjeldahl method (Bremner, 1965 a,b). A 2 g sample of finely ground soil was analysed using semimicro-Kjeldahl equipment.

Tissue subsamples for P and Al were ashed at 450°C and dissolved in dilute HCl. Phosphorus was analysed colorimetrically as described above and Al was determined by atomic absorption spectrophotometer. Total N was determined by the salicylic acid modification of the Kjeldahl method (Bremner, 1965a). Standard tissue samples were included in every set.

Isotope analyses

Cerenkov radiation was used to determine ^{32}P activity (Haberer, 1966). A 0.5 g foliage sample was ashed at 450°C, dissolved in 4 N HCl, transferred quantitatively into polyethylene liquid scintillation tubes, and made up to a standard volume with water. These were counted for 30 minutes in a model 314 Ex, Pachard Tri-carb liquid scintillation instrument. Total P was determined on these same samples using the method described above. All counts were corrected for isotope half life and reported as counts per minute per gram (cpm/g).

The ^{15}N atom percent was determined by mass spectrometer as described by Bremner (1965b). Two mass spectrometer instruments were employed. Samples of soils and tissue

samples to study initial uptake and the distribution in the ecosystem at harvesting were analysed at the Tennessee Valley Authority, Muscle Shoals, Alabama. Samples collected to follow seasonal foliage changes were analysed by P. J. Eberhardt at the University of Arizona, Tucson, Arizona. In all cases results were corrected by comparison with standard ^{15}N samples (0.366 and 0.995 atom percent). A standard pine tissue sample was also run periodically.

Data Calculations

The figures obtained from the mass spectrometer determinations were expressed in atom percent ^{15}N, i.e.,

$$\text{N atom percent} = \frac{(\text{number of } ^{15}N \text{ atoms})\ 100}{\text{number of } ^{14}N + ^{15}N \text{ atoms}}$$

$$= \frac{(\text{equivalents } ^{15}N)\ 100}{\text{equivalents } (^{14}N + ^{15}N)}$$

Total N contained in a component was calculated from its dry weight and N concentration. It may be expressed in either grams or equivalents (eq). If the weight is in grams then:

$$\text{Total N content (meq)} = A = \frac{\%\ N \times wt}{1.4}$$

If x = meq N in the component derived from the tagged fertilizer

y = meq N in the component derived from the soil

a = atom percent ^{15}N of the tagged material

b = atom percent ^{15}N in an equivalent sample from an untreated plant

c = atom percent ^{15}N in fertilized plant

Then

$$x + y = A$$

and

$$ax + by = cA$$

These basic equations are solved to eliminate y and rearranged to give

$$x/A = \text{fraction of total N from fertilizer} = \frac{c-b}{a-b}$$

This equation is useful in intrepreting data when biomass is not available. It was used in the study of initial uptake and seasonal trends in foliage ^{15}N.

If biomass data are available then

$$x = \frac{A(c-b)}{a-b}$$

Furthermore, if Z meq N were applied, then the percent recovery may be calculated.

$$\text{Percent recovery of applied N} = \frac{100\ x}{Z}$$

Nitrogen concentration and ^{15}N atom percent may be used to calculate the μeq ^{15}N absorbed per gram

$$\mu\text{eq } ^{15}N \text{ absorbed per gram tissue} = \frac{\%\ N\ (c-b)}{0.14}$$

This calculation was made for the studies on initial uptake and long-term foliage changes. It is particularly useful to compare with ^{32}P data (cpm/g) as both refer to the

quantity of nutrient derived from the fertilizer when expressed on per unit dry weight of tissue.

Standard methods of statistical analysis were used (Steel and Torrie , 1960). Estimated mean squares were obtained using the method described by Hicks (1964) in order to determine the appropriate F tests. Details of individual statistical analyses are given where appropriate.

RESULTS

Initial Uptake of N and P

The uptake of N and P from fertilizers was followed over 10 weeks using labelled materials. Foliage samples, collected at periodic intervals from several crown positions and ages of foliage, were analysed for N and P concentrations and ^{15}N and ^{32}P isotope levels. The P data for the first day after treatment are not included because of procedural problems. However, as no substantial uptake of ^{32}P occurred until after the 11th day, this omission is not considered critical. Details of the statistical analysis are given in Appendix B.

In the subsequent discussion the term location-in-crown is taken to include level in crown, branch order and foliage age. The terms position-in-crown or crown position are defined as including crown level and branch order but excluding foliage age. There were three crown levels; terminal (leader), upper crown, and lower crown (branches). There were two orders of branches (first and second) and three foliage ages. Foliage ages are denoted by the year they were initiated, but where pertinent are also described as current, 1-year-old, or 2-year-old.

Total N and P Concentrations

The P concentration in the foliage did not vary significantly

with position-in-crown, but the older 1967 and 1968 foliage had higher P levels (Table 3 and Appendix B). The mean P concentrations were 0.14, 0.16, and 0.17 percent in the current, one-year-old, and two-year-old foliage respectively.

The N concentrations in the upper crown branches were significantly higher than in the lower crown (Table 3). However, the differences may reflect tissue age rather than differences in N concentration due to crown position. In the single degree of freedom contrast, the lower branches were more heavily weighted in favor of the 1968 and 1969 foliage ages. These one- and two-year-old foliage groups had a mean N concentration of 0.90 and 0.77 percent, compared to the 1.00 percent N in the current foliage. Foliage ages were significantly different. The analysis of variance of N concentration in the 1969 foliage did not show a significant difference due to crown position.

The concentration of N in the foliage increased significantly with time (Tables 3,4). In particular the N concentration in the current (1969) foliage rose rapidly in the first 11 days (Figure 7). There was also a significant location-in-crown x time interaction which may be explained by the relative differences between foliage ages changing with time (Figure 7). In the analysis of the 1969 foliage the position-in-crown x time interaction was not significant.

The mean P concentration was stable over the first 71 days (Table 4). However, there was a significant location-in-crown x time interaction. This was partially

Table 3. Summary of the analysis of variance of the initial uptake of N and P into slash pine foliage.

Source	Total P	^{32}P cpm/g	Total N	^{15}N atom %	μeq ^{15}N absorbed/g	% uptake N
	Significance level					
	All ages of foliage					
Location-in-crown (A)	*	***	***	***	***	***
Day (B)	ns	***	***	***	***	***
Tree (C)	***	***	***	***	***	***
A x B	***	***	*	***	***	***
A x C	***	***	ns	***	**	***
B x C	***	***	ns	***	***	***
Subdivision of A (single df contrasts)						
Terminal vs other locations	ns	***	ns	***	***	***
Upper br. vs lower branches	ns	***	***	***	***	***
Upper 1st-order vs upper 2nd-order	ns	ns	ns	ns	ns	ns
Lower 1st-order vs lower 2nd-order	ns	ns	ns	ns	**	ns
Age 1969 vs 1967+1868	***	*	***	***	***	***
Age 1967 vs 1968	ns	ns	***	ns	***	ns

Table 3. continued

Source	Total P	^{32}P cpm/g	Total N	^{15}N atom %	µeq ^{15}N absorbed/g	% uptake N
	Significance level					
			(2) 1969 foliage only			
Position-in-crown (A)	ns	*	ns	**	**	**
Day (B)	**	***	***	***	***	***
Tree (C)	***	**	ns	ns	ns	ns
A x B	ns	***	ns	***	***	***
A x C	***	**	ns	*	ns	*
B x C	***	ns	ns	ns	ns	ns
Subdivision of A (single df contrast)						
Terminal vs other positions	ns	*	ns	**	**	**
Upper br. vs lower branches	ns	*	ns	***	***	**
Upper 1st-order vs upper 2nd-order	ns	ns	ns	ns	ns	ns
Lower 1st-order vs lower 2nd-order	ns	ns	ns	ns	*	ns

ns Not significant.
* Significant at 5 percent level.
** Significant at 1 percent level.
*** Significant at 0.1 percent level.

Table 4. Summary of changes in N and P concentrations and ^{15}N and ^{32}P isotope levels in the tree crowns during the initial 71 days after fertilization.

Days after application	P	N	^{32}P	^{15}N	^{15}N absorbed/g	Fertilizer N
	____ % ___		cpm/g	atom %	µeq	% of total
1		0.80		0.367	0.00	.01
5	0.15	0.84	10	0.368	0.00	.02
11	0.16	0.93	91	0.383	0.10	.74
21	0.16	0.92	489	0.472	0.69	5.12
35	0.16	0.98	1747	0.672	2.16	15.03
49	0.16	0.97	2639	0.763	2.78	19.55
71	0.15	0.92	4588	0.785	3.02	21.44

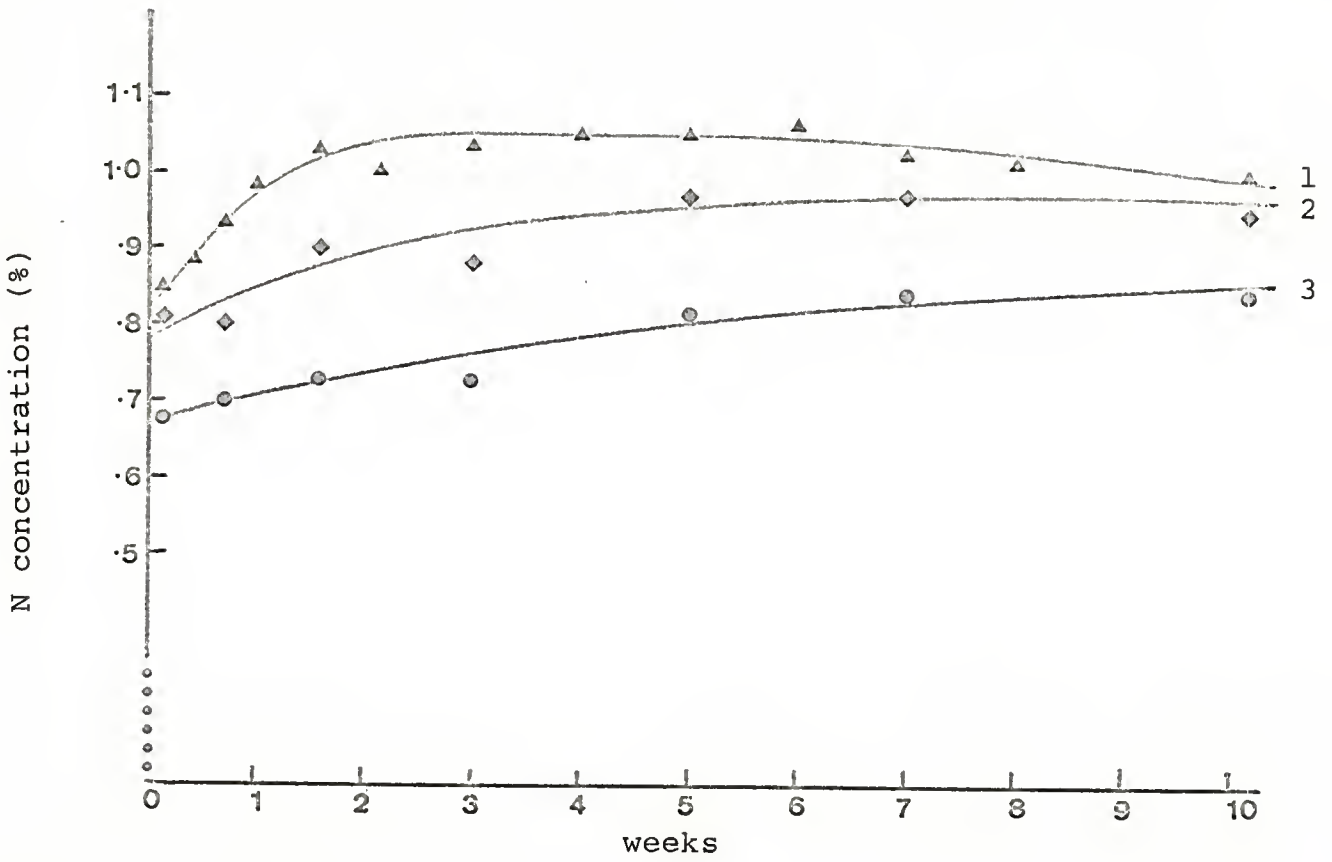

Figure 7. Changes in the foliage N concentration during the initial 10 weeks after fertilizer application. 1, 2, and 3 are needles initiated in 1969, 1968, and 1967, respectively.

explained by a drop in the P concentration of the current (1969) foliage together with a slight rise in the older foliage (Figure 8). Location-in-crown also included crown position and there was evidence that P concentrations in older foliage form various crown positions changed with time (Appendix B, Table 27). Thus, 5 days after fertilizer application, the 1968 foliage from the terminal leader, upper crown, and lower crown branches had 0.150, 0.157, and 0.154 percent P. After 71 days the P concentrations in 1968 foliage from these same crown levels were 0.146, 0.152, and 0.170 percent, respectively. The P concentration also had significant tree x time and trees x location-in-crown (or trees x position-in-crown) interactions. These interactions indicated that the two trees were dissimilar.

Isotope Uptake

The amount of ^{15}N in the foliage was expressed in several ways, but initially the μeq ^{15}N absorbed per gram of tissue will be considered as this is comparable to ^{32}P cpm/g.

The first indication of the tracers reaching the crown was 5 to 7 days after fertilization (Table 4). Both isotopes reached the lower crown first (Appendix B, Table 27). The level of isotopes increased gradually at first, but rose rapidly after the 15th day. Phosphorous uptake into foliage was linear with time after the 3rd week (Figure 9). The linear relationship is clearly demonstrated by the regression equations and their respective coefficients of determination (Table 5). In contrast N uptake showed a distinct

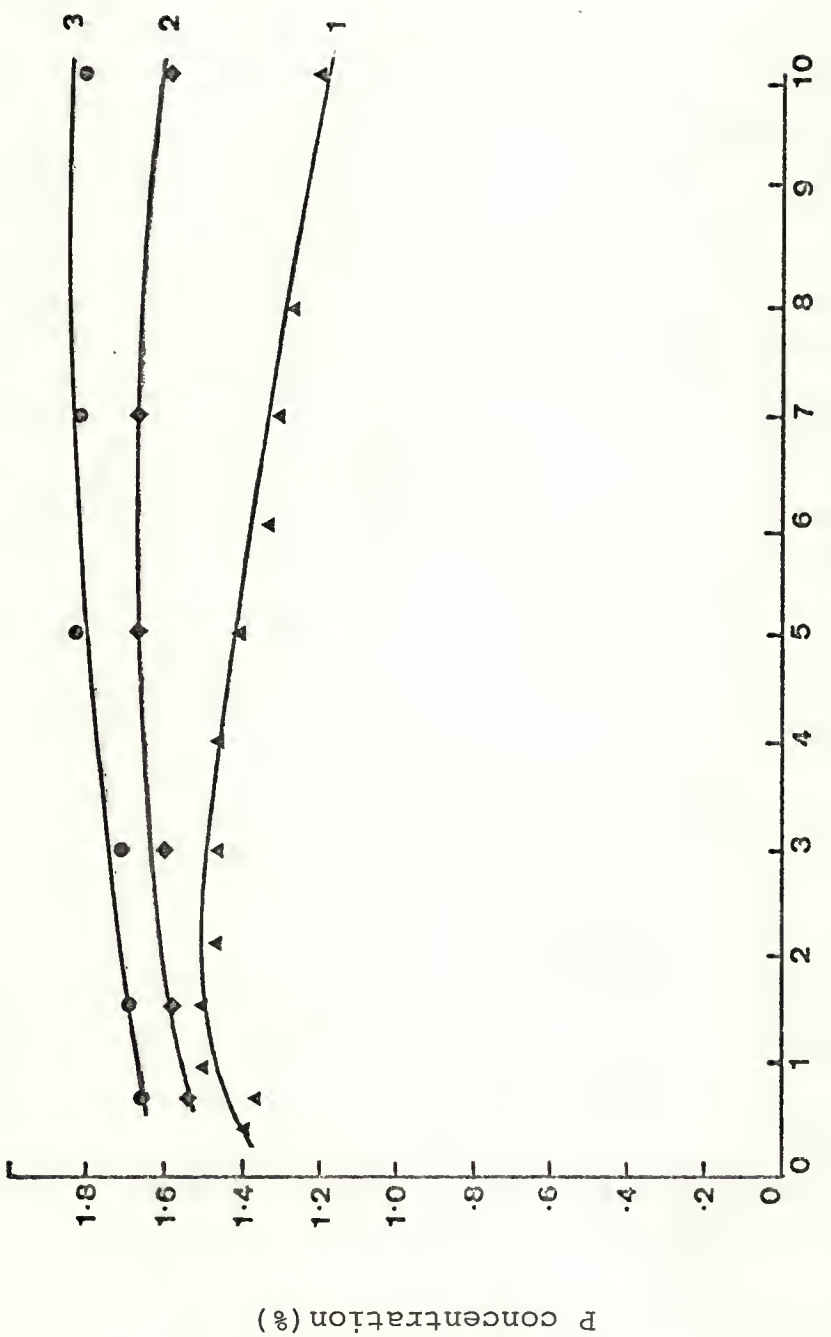

Figure 8. Changes in the foliage P concentration during the initial 10 weeks after fertilizer application. 1, 2, and 3 are needles initiated in 1969, 1968, and 1967, respectively.

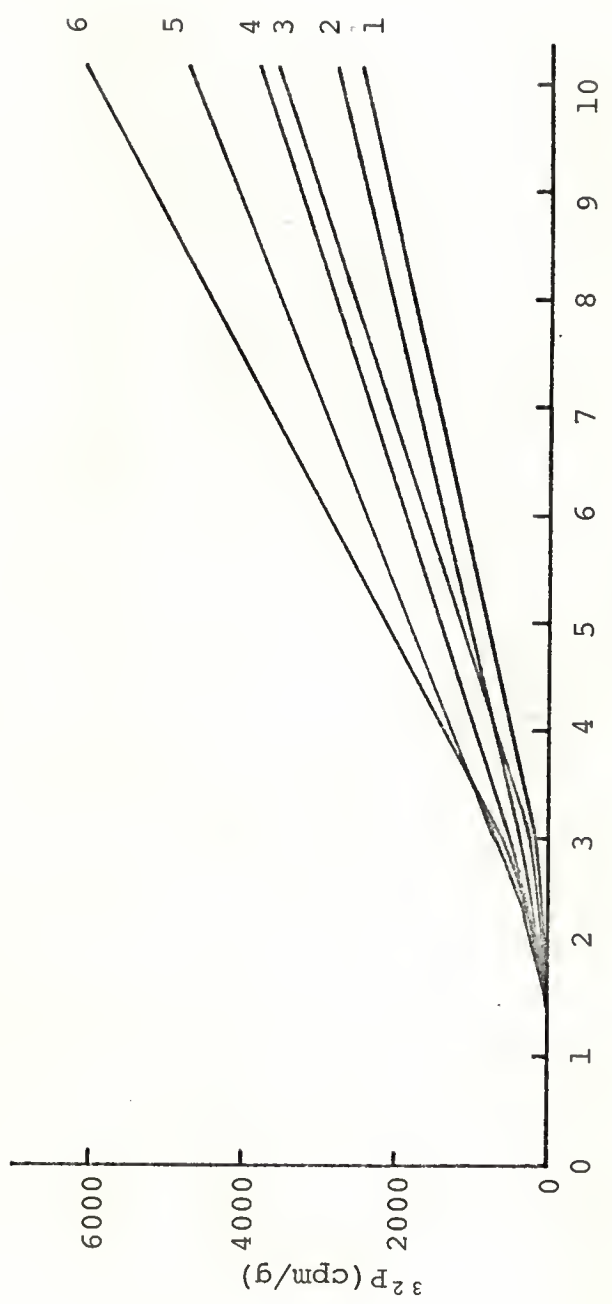

Figure 9. The uptake of ^{32}P into various parts of the crown during the initial 10 weeks after fertilization. 1 and 2 are 1969 and 1968 needles from leader; 3 and 4 are 1969 and 1968 needles from upper crown branches; 5 and 6 are 1969 and 1968 needles from lower crown branches, respectively.

Table 5. Regression equations of ^{32}P uptake into various locations in the crown between 3 and 10 weeks.

Position-in-crown	Foliage age	Regression[a]	R^2
Terminal	1969	y = 46.52x - 835	0.935***
Terminal	1968	y = 47.67x - 636	0.969***
Upper	1969	y = 65.98x - 1135	0.949***
Upper	1968	y = 66.53x - 899	0.816**
Lower	1969	y = 80.10x - 982	0.834***
Lower	1968	y = 109.11x - 1666	0.964***
Lower	1967	y = 110.21x - 1825	0.945***

** Significant at 1 percent level.[b]

*** Significant at 0.1 percent level.

[a]y is in cpm/gram.

x is time in days after application.

The test for significance of R^2 is

$$F^{1}_{n-2} = \frac{(n - 2)R^2}{(1 - R^2)}$$

where n is number of observations.

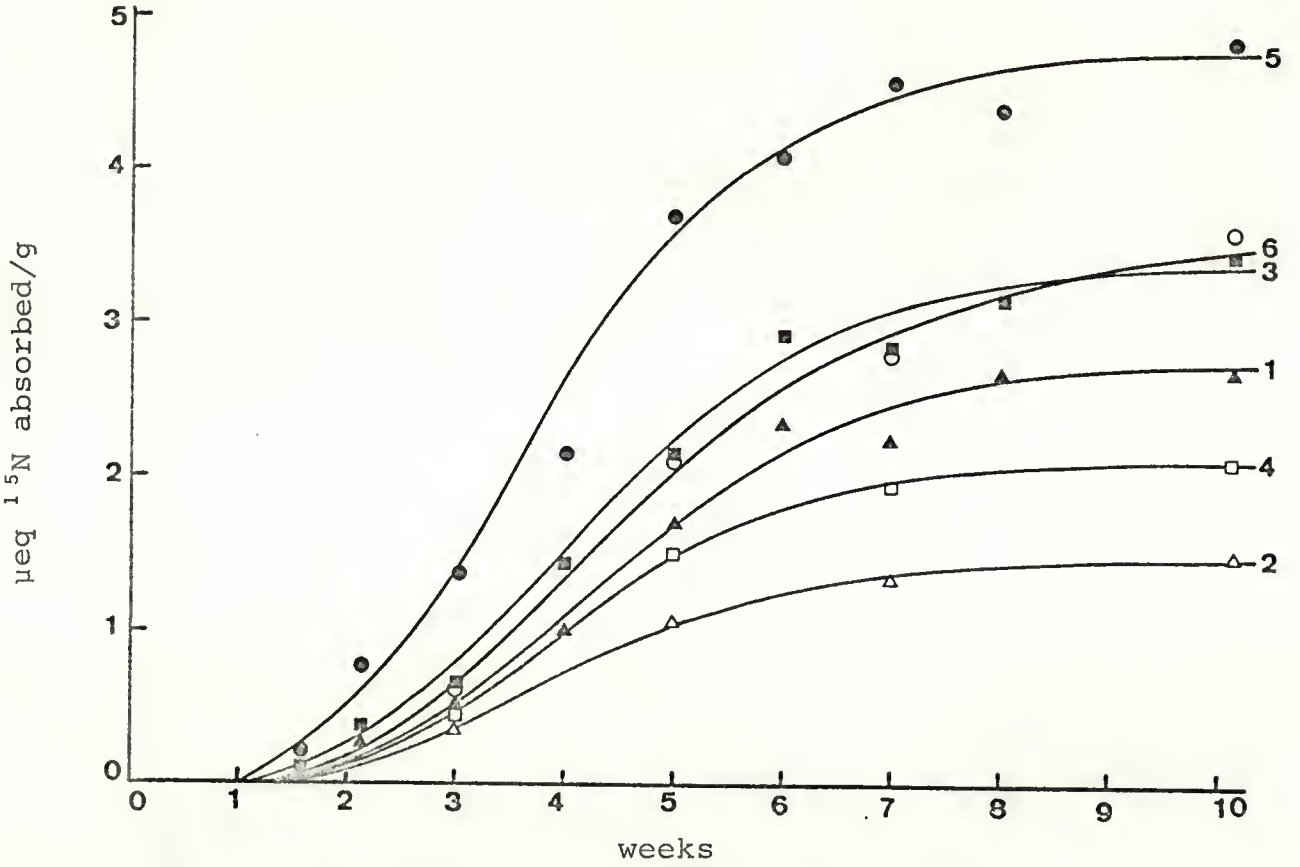

Figure 10. The uptake of ^{15}N into the various parts of the tree crown during the initial 10 weeks after fertilization. 1 and 2 are 1969 and 1968 needles from the leader; 3 and 4 are 1969 and 1968 needles from upper crown branches; 5 and 6 are 1969 and 1968 needles from the lower crown branches, respectively.

decline after 6 to 7 weeks. The maximum rate of N uptake was between the 3rd and 5th week (Figure 10).

Isotope levels were consistently greater in the lower crown than in the upper or terminal leader (Figures 9, 10). The first- and second-order branches were not significantly different.

The level of ^{32}P was greater in older foliage than in the current (1969) flush (Table 6). In contrast, ^{15}N accumulated in greater amounts in current foliage than in one- (1968) or two-year-old (1967) foliage. These differences between foliage ages were highly significant (Table 3).

The interaction of location-in-crown x time was significant for both isotopes and resulted from the difference in isotope levels between various crown positions increasing with time (Figures 9, 10). After the third week the difference in ^{32}P levels, between foliage ages at a particular crown level, sometimes remained relatively constant with time (Figure 9). Thus the difference between ^{32}P activity in the 1968 and 1969 foliage in the upper crown and leader, and between the 1967 and 1968 foliage in the lower crown tend to be constant. The slopes of the regression line of ^{32}P activity against time also show this feature (Table 5). However, ^{32}P activity in the lower current (1969) needles did not parallel the activity in the lower, older foliage with time.

Correlations between ^{32}P activity and μeq ^{15}N absorbed per gram were also calculated to determine if the accumulation

Table 6. Summary of N and P concentrations in the initial uptake of N and P into tree crowns by position and foliage age.

Position in crown	Foliage age	P	N	^{32}P	^{15}N	^{15}N absorbed	Fertilizer N
		%		cpm/g	atom %	µeq	% of total
Terminal	1969	0.15	1.03	696	0.508	1.05	6.93
	1968	0.15	0.84	1,058	0.470	0.62	5.09
Upper crown 1st-order	1969	0.14	1.00	982	0.556	1.34	9.31
	1968	0.16	0.85	1,369	0.504	0.87	6.76
Upper crown 2nd-order	1969	0.14	.94	1,051	0.558	1.29	9.40
Lower crown 1st-order	1969	0.13	1.00	1,380	0.613	1.87	12.14
	1968	0.16	0.95	2,028	0.533	1.20	8.19
	1967	0.18	0.76	1,922	0.534	0.97	8.20
Lower crown 2nd-order	1969	0.14	1.01	1,553	0.652	2.23	14.07
	1968	0.16	0.96	2,191	0.540	1.30	8.52
	1967	0.17	0.77	1,704	0.554	0.94	9.21
Mean	1969	0.14	1.00	1,132	0.577	1.56	10.37
	1968	0.16	0.90	1,674	0.512	1.00	7.14
	1967	0.17	0.77	1,818	0.544	0.95	8.70

of the two isotopes in foliage were related. Correlations were calculated for each separate sampling date from the 11th day, rather than for all crown locations and all days. The uptake with time is strongly influenced by availability of the isotope from the soil. This factor was removed by considering sampling dates separately. All correlations were non-significant, whether based on all ages of foliage, or current foliage only (Table 7). Furthermore, Fisher's Z test failed to show that the correlation coefficients differed (Snedecor, 1956). The pooled estimate of the correlation, based on 131 degrees of freedom, was -0.0637. Both trees were considered at any one date, and since the trees differed in the uptake of isotopes, this may have reduced the correlation coefficients, particularly where current foliage was analyzed.

The ^{15}N results are also expressed in terms of atom percent and percent of total N that came from the fertilizer. The overall trends in these data are similar, but other points are emphasized.

At the end of 10 weeks 18.6 percent of the N, in the current (1969) foliage of the terminal leader, had been derived from the fertilizer. At the lower crown levels a greater proportion of the N had come from the fertilizer; the values were 24.9 and 32.0 percent in the current foliage of the upper and lower crowns respectively.

The percent N from the fertilizer was greater in the younger foliage. At the end of 10 weeks some 26 percent of

Table 7. Correlation between μeq ^{15}N/g absorbed and ^{32}P cpm/g during initial uptake.

Day	Number of observations	r
11	22	0.1633
15	10[a]	0.0837
21	22	-0.2344
28	10	0.0062
35	22	-0.2442
42	10	0.2663
49	22	-0.1323
56	10	0.2977
71	21[b]	-0.2112

[a] On alternate days only 1969 foliage was collected so there are fewer observations.

[b] One missing observation.

the N in the current (1969) foliage and 17.6 and 21.5 percent in the 1968 and 1967 foliage, respectively, had been derived from the fertilizer. The difference between the 1967 and 1968 foliage was not significant.

Long-Term Foliage Changes

The three foliage ages were statistically analysed as separate units using a split-plot in time model (Appendix C). There was no direct statistical comparison between foliage ages. All three N treatments were included in the statistical analysis of needle weight, weight per cm length of needle, concentrations of N, P, and Al, P to Al weight ratio, and N and P content on a needle and per unit length of needle basis (Table 8). The treatment sum of squares were partitioned into linear and quadratic components. The parameters which included ^{15}N measurements (percent of total N from fertilizer, μeq ^{15}N absorbed per gram, μeq ^{15}N absorbed per needle, μeq ^{15}N absorbed per cm of needle) did not include the control or pretreatment data. Consequently partitioning of the sum of squares for treatment was not possible.

Foliage Initiated in 1968

This foliage was shed from the trees during the spring following fertilizer application.

The N concentration showed a significant linear and quadratic treatment response. Thus the mean N concentrations were 0.85, 0.72, and 0.75 percent in the high-N (224 kg N/ha), low-N (56 kg N.ha), and control treatments. The effect of time and the time x treatment interaction was also significant (Figure 11). The foliage N concentration in high-N treatment rose rapidly during the first 12 weeks, after

Table 8. Summary of the analysis of variance of the long-term changes in needle weight and in N, P, Al and ^{15}N levels in the 1968, 1969 and 1970 issues of foliage, as influenced by N treatment and sampling date.

	Needle Dry Weight	Needle wt/cm length	Concentration			P to Al ratio	N from fertilizer[a]		N content			content/cm needle		
			% N	% P	ppm Al		% of total N[b]	µeq ^{15}N absorbed/g	N	P	µeq ^{15}N absorbed/g	N	P	µeq ^{15}N absorbed[a]
	significance level													
Foliage initiated 1968														
Treatment (A)	ns	ns	**	ns	ns	*	**	**	ns	ns	**	ns	ns	**
Linear	ns	ns	**	ns	ns	ns			ns	ns		ns	ns	
Quadratic	ns	*	*	ns	ns	*			ns	ns		ns	ns	
Time (B)	*	ns	**	*	ns	ns	ns	ns	*	ns	ns	**	ns	ns
A x B	ns	ns	**	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Foliage initiated 1969														
Treatment (A)	ns	ns	***	ns	ns	ns	***	***	*	ns	***	*	ns	***
Linear	ns	ns	***	ns	ns	ns			*	ns		**	ns	
Quadratic	ns	ns	**	*	ns	ns			ns	ns		ns	ns	
Time (B)	***	***	***	**	***	***	**	***	***	***	***	***	***	***
A x B	ns	ns	ns	ns	ns	ns	ns	**	ns	ns	***	ns	ns	**
Foliage initiated 1970														
Treatment (A)	ns	ns	ns	ns	ns	ns	***	***	ns	ns	***	ns	ns	***
Linear	ns	ns	ns	ns	ns	ns			ns	ns		ns	ns	
Quadratic	ns	*	ns	ns	ns	ns			ns	ns		ns	ns	
Time (B)	***	***	***	**	***	***	**	**	***	***	***	***	***	***
A x B	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	***	ns	ns	*

[a] ns, *, **, *** described in Appendix C, page 184.
Control and pretreatment (initial) samples not included in analysis.
[b] This analysis and that of ^{15}N atom percent similar as the data only differ by constants.

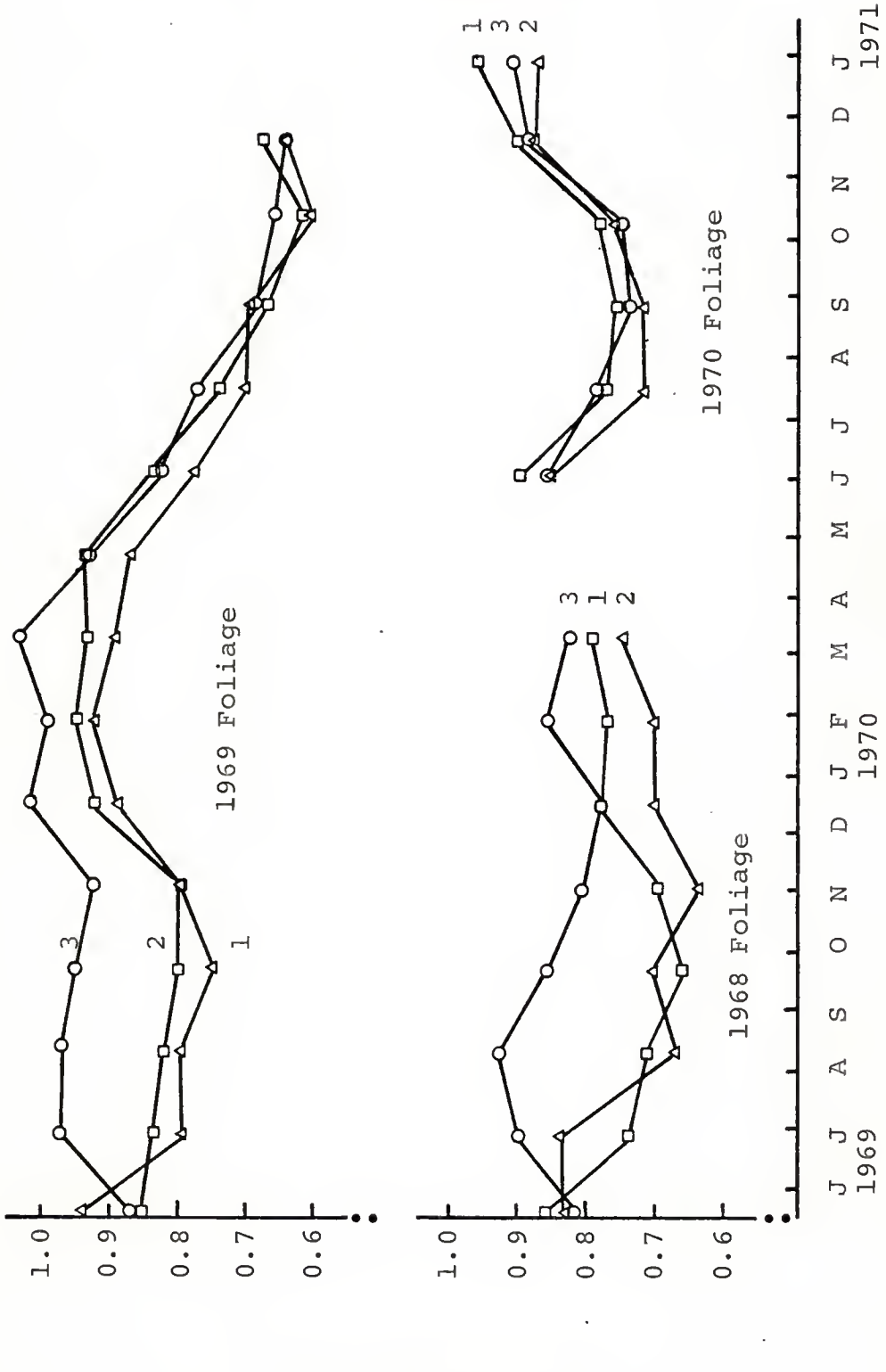

Figure 11. The changes in N concentration of needles initiated in 1968, 1969, and 1970, as influenced by season and fertilizer treatment. 1, 2, and 3 are control, low-N, and high-N treatments, respectively.

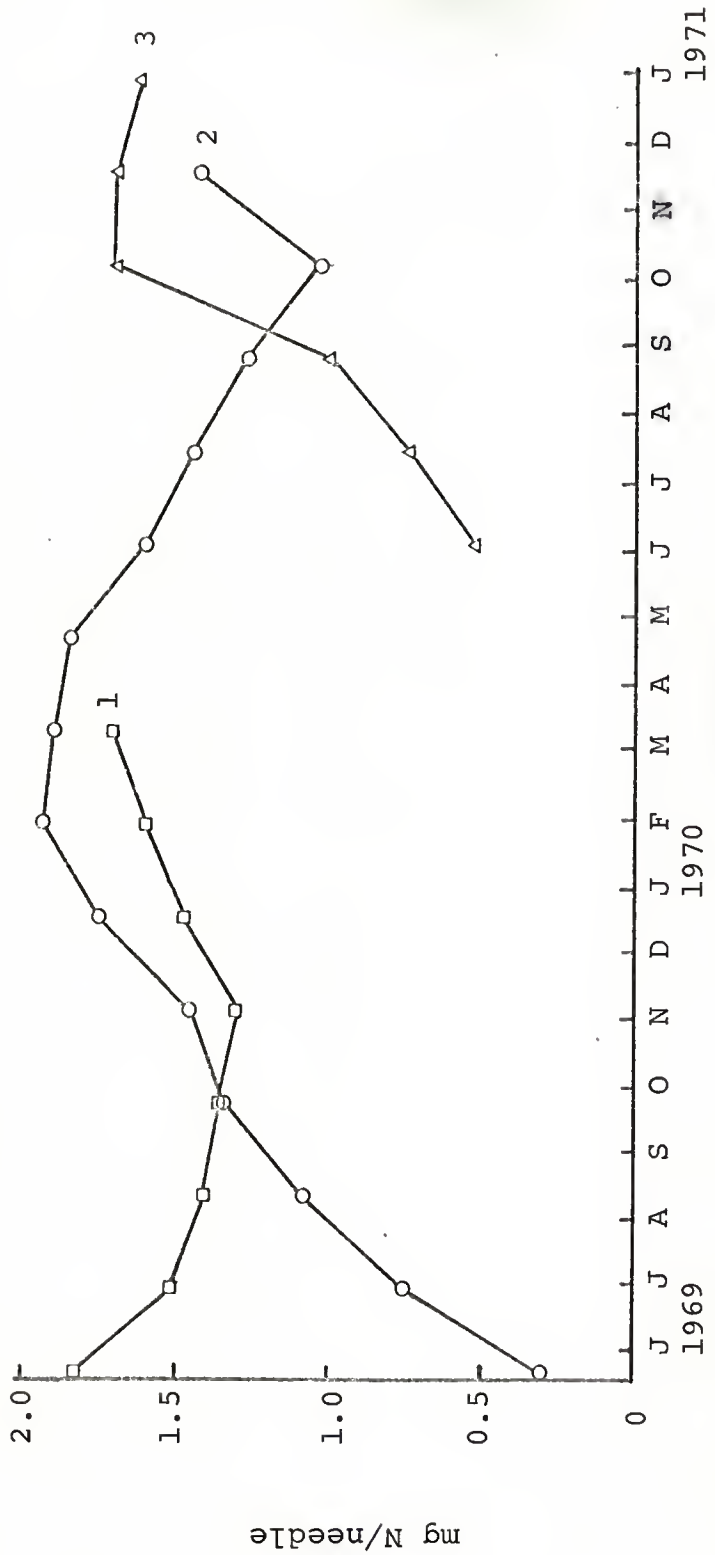

Figure 12. The changes in N content of the needles over two growing seasons. 1, 2, and 3 indicate needles initiated in 1969, 1970, and 1971, respectively.

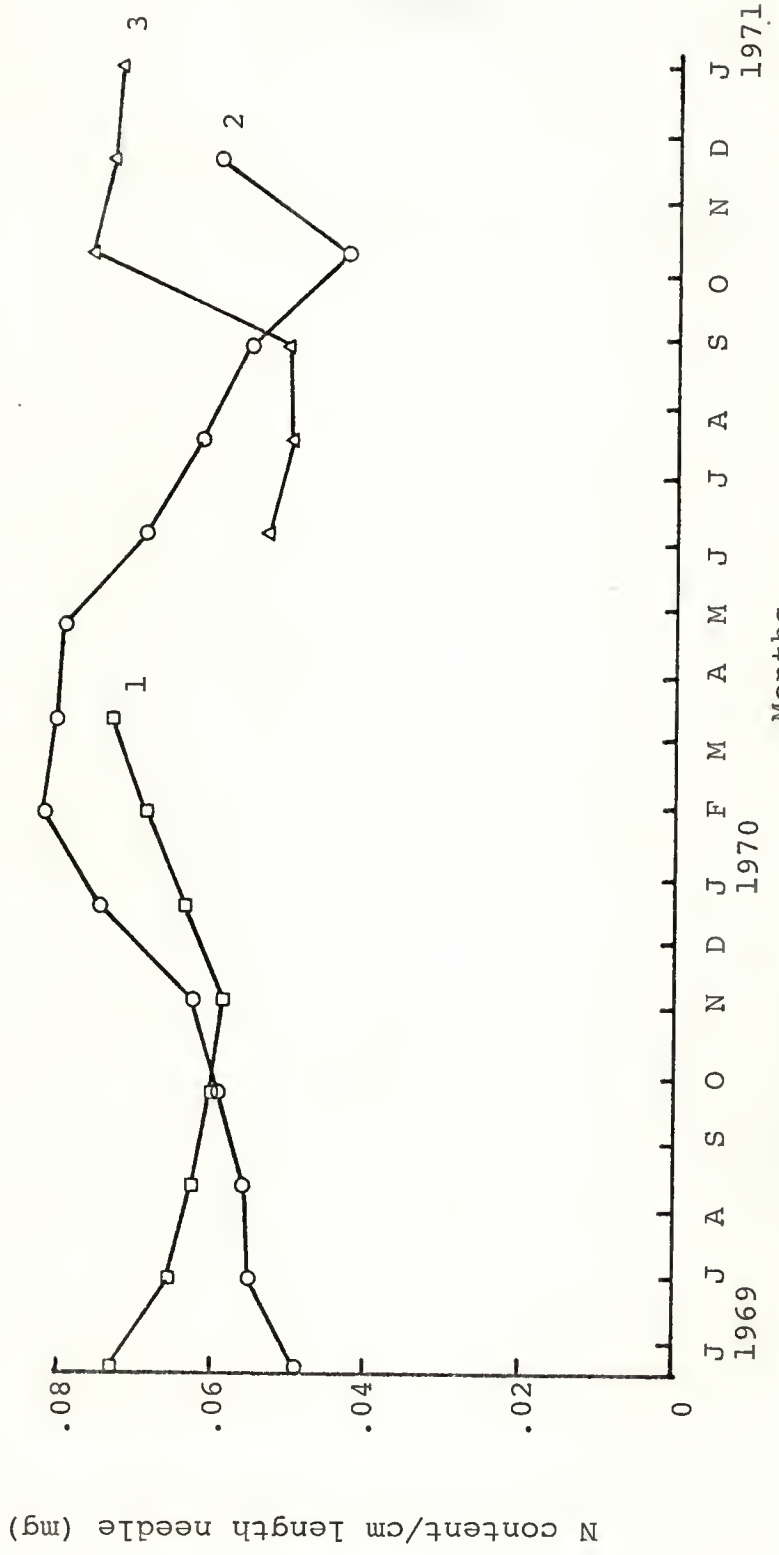

Figure 13. Changes in the N content per cm length of needle over two growing seasons. 1, 2, and 3 indicate needles initiated in 1968, 1969, and 1970, respectively.

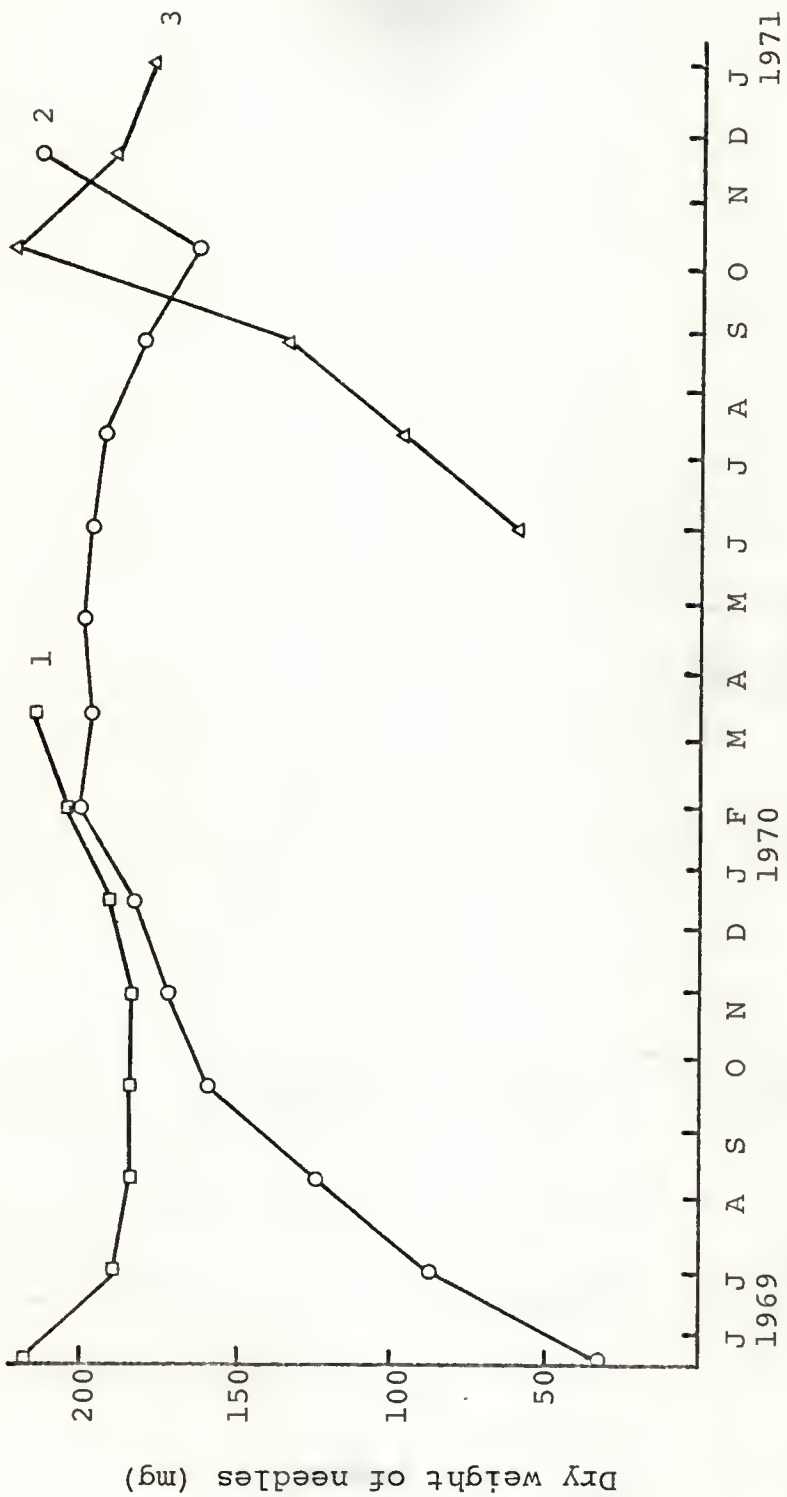

Figure 14. Changes in the dry weight of needles over two growing seasons. 1, 2, and 3 are needles initiated in 1968, 1969, and 1970, respectively.

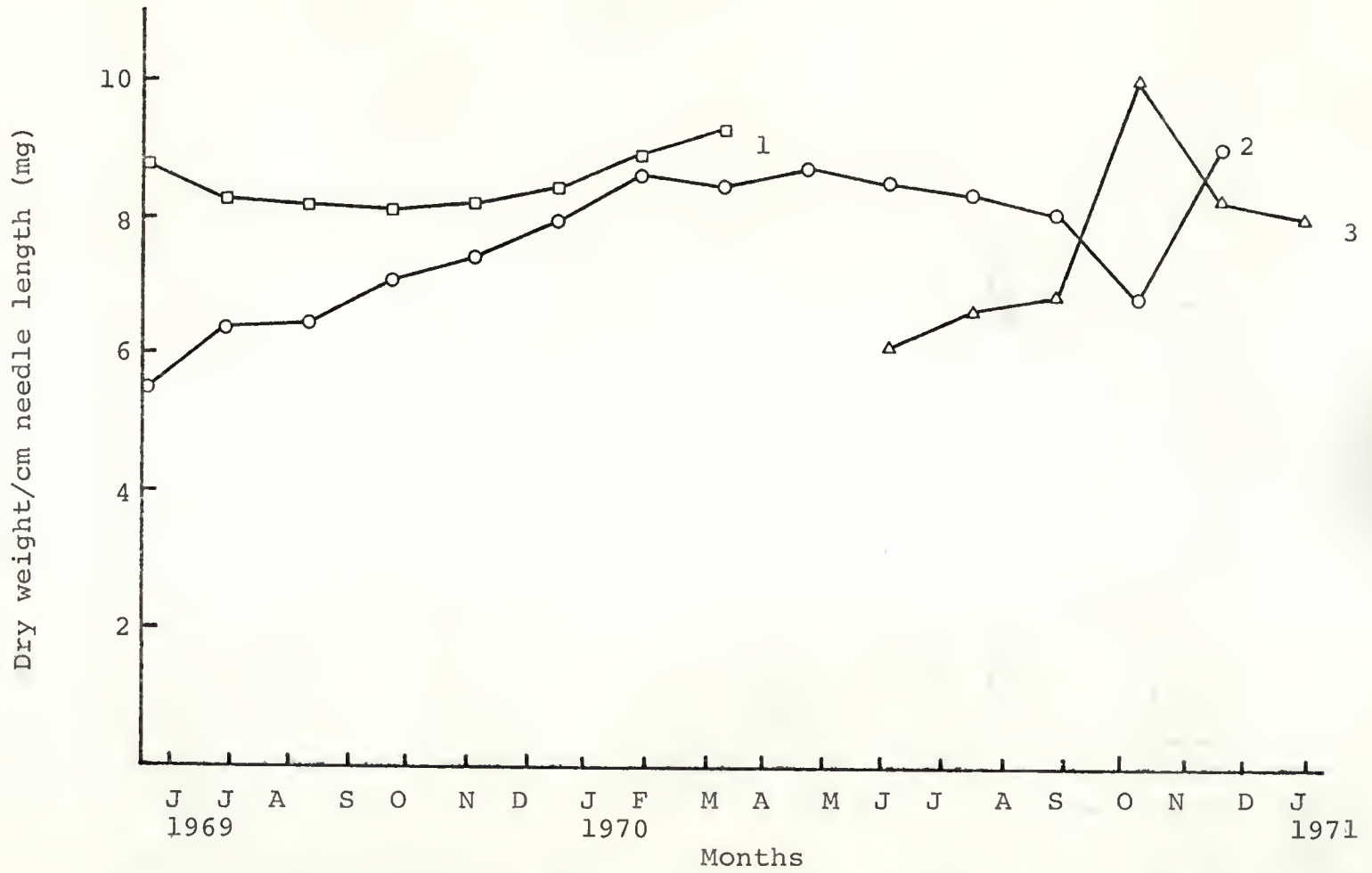

Figure 15. The changes in dry weight per cm needle length over two growing seasons. 1, 2, and 3 are needles initiated in 1968, 1969, and 1970, respectively.

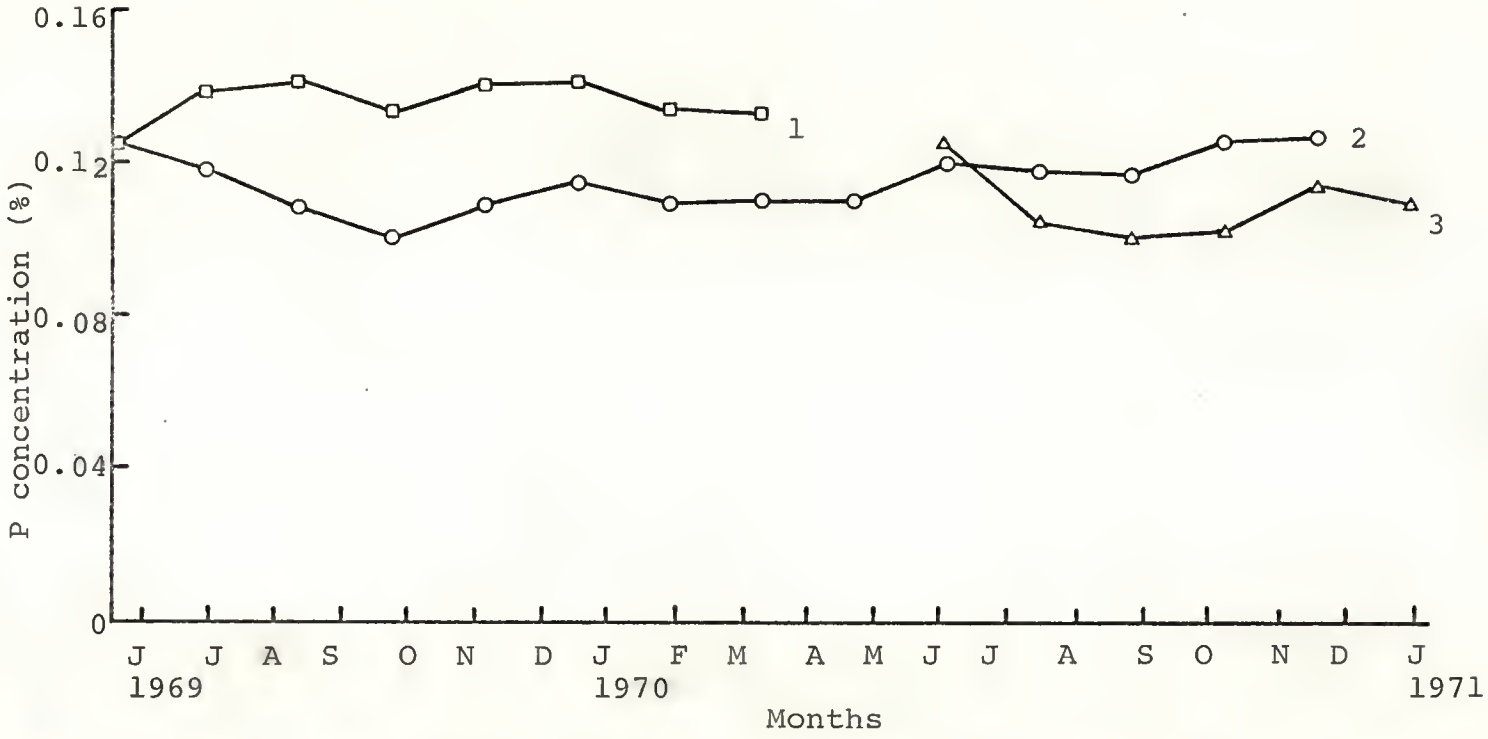

Figure 16. The changes in P concentration in needles over two growing seasons. 1, 2, and 3 are needles initiated in 1968, 1969, and 1970, respectively.

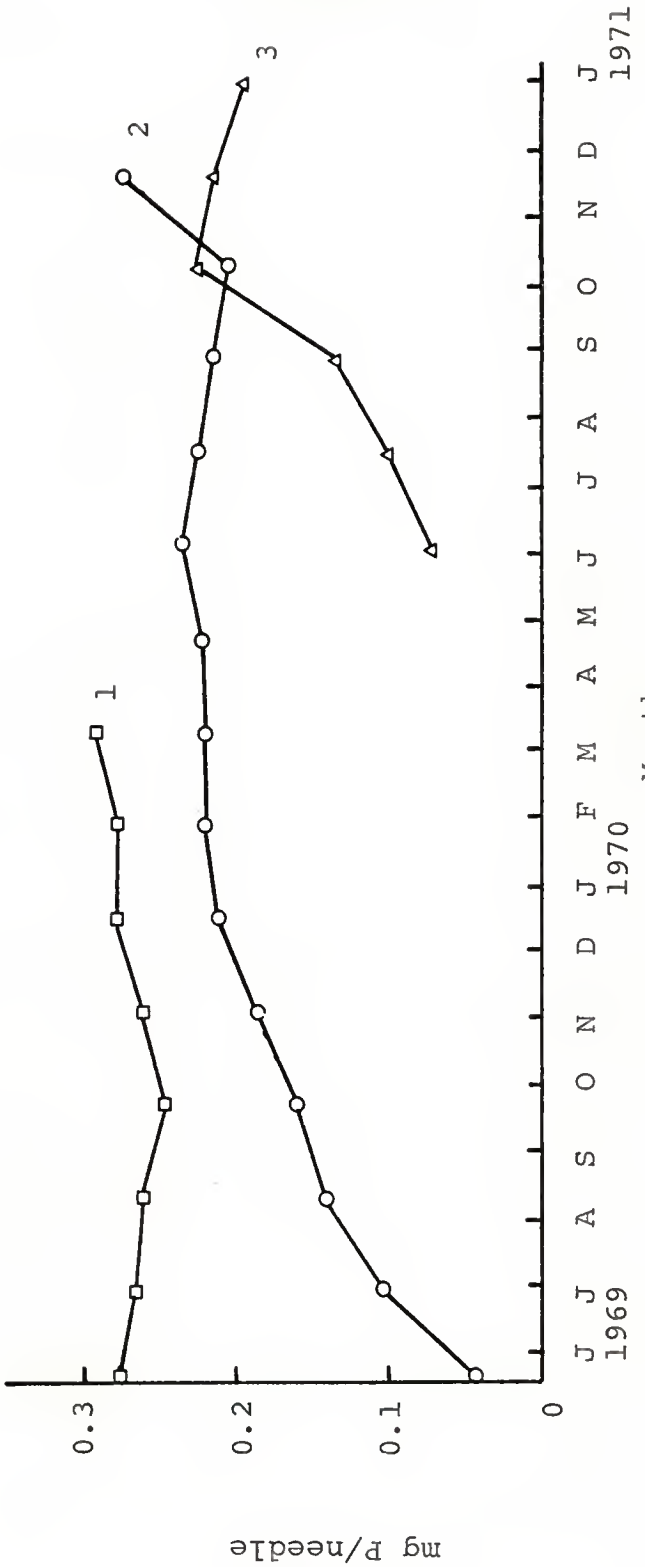

Figure 17. The changes in the amount of P in the needles over two growing seasons. 1, 2, and 3 are needles initiated in 1968, 1969, and 1970, respectively.

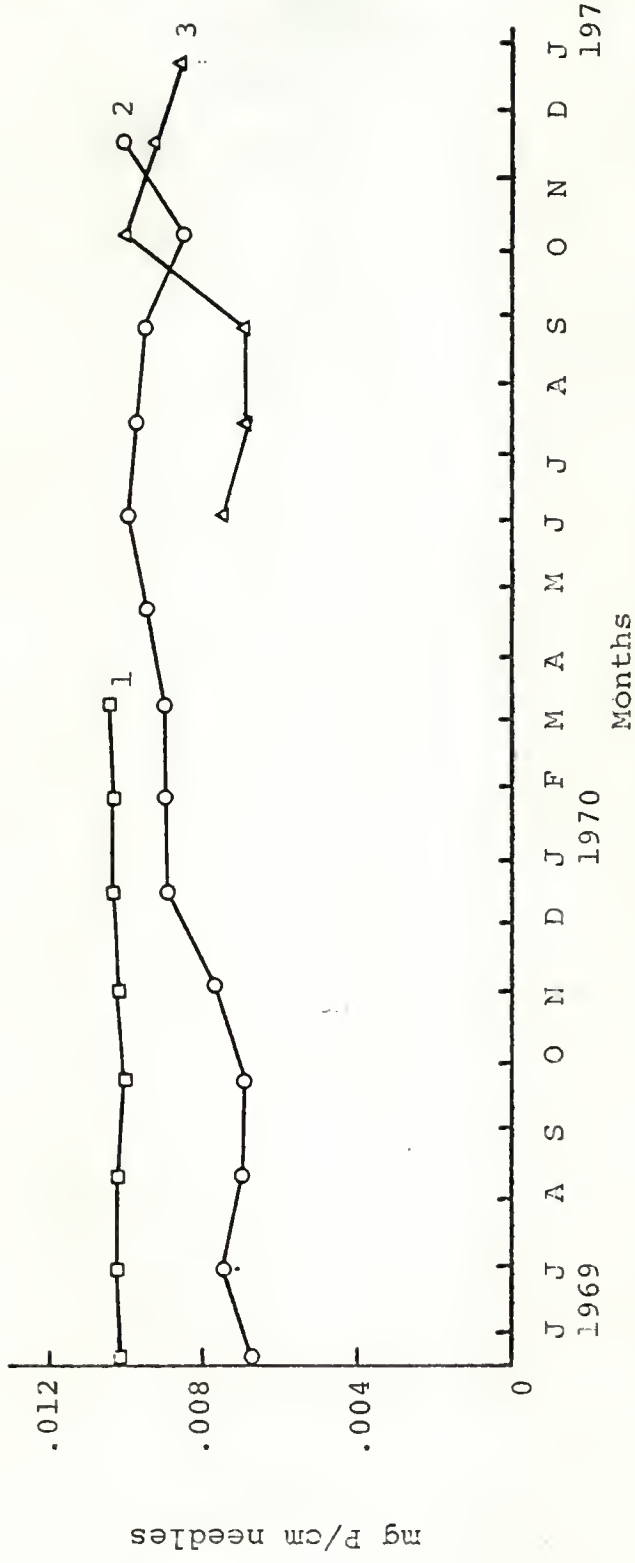

Figure 18. The changes in P content per cm needle over two growing seasons. 1, 2, and 3 are needles initiated in 1968, 1969, and 1970, respectively.

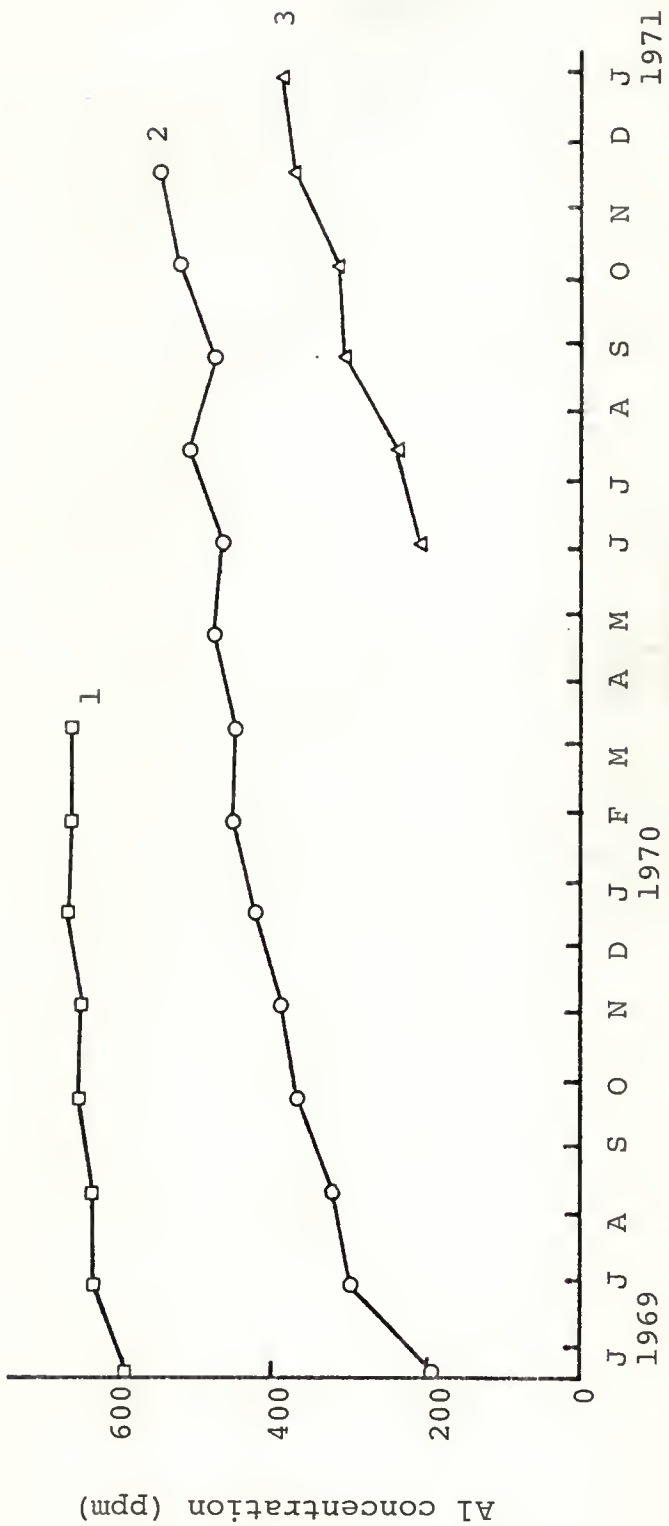

Figure 19. The changes in Al concentrations in the needles over two growing seasons. 1, 2, and 3 are foliage initiated in 1968, 1969, and 1970, respectively.

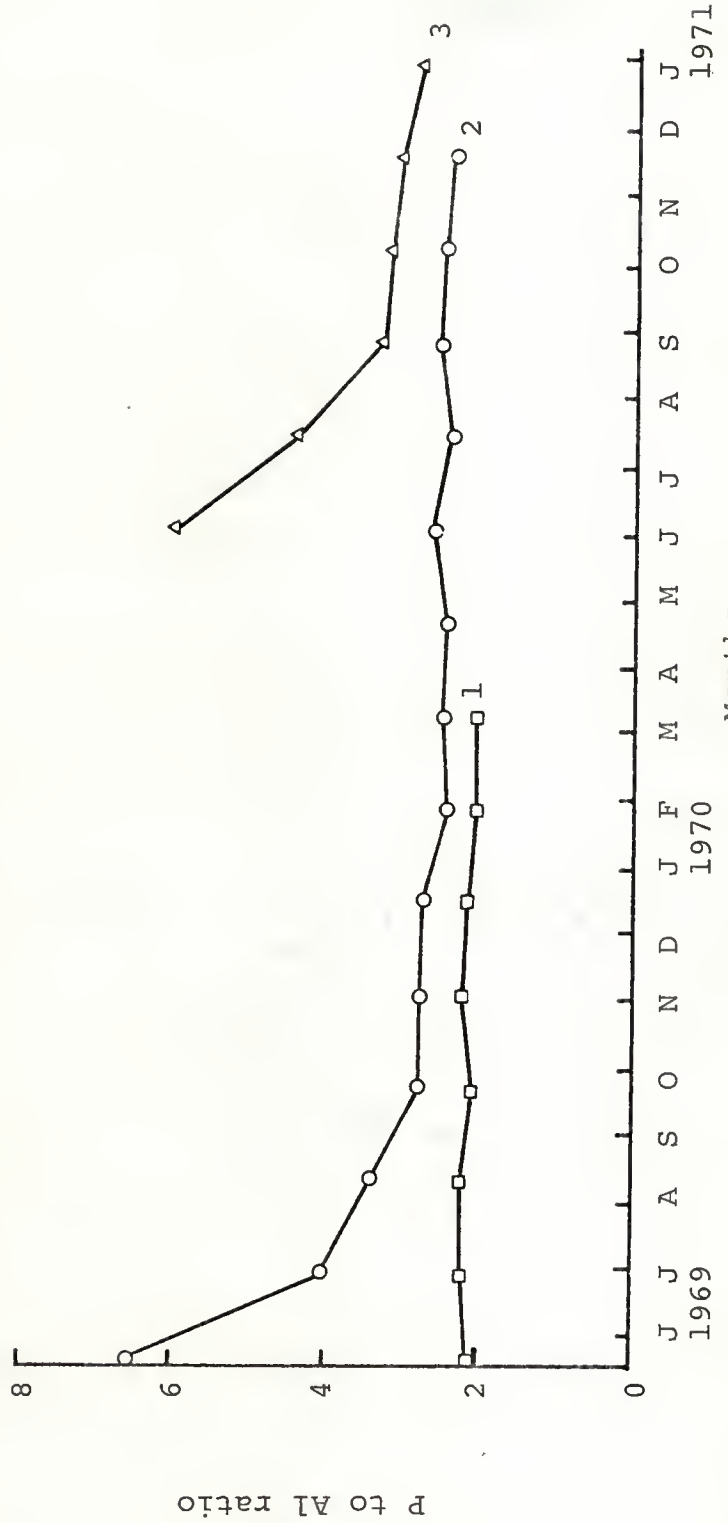

Figure 20. The changes in P to Al ratio in the needles over two growing seasons. 1, 2, and 3 are needles initiated in 1968, 1969, and 1970, respectively.

it tended to decline with time. In the low-N and control trees, the level of N dropped for the first 20 weeks and subsequently began in increase slightly.

The dry weight and N content per needle or per cm of needle were generally not influenced by N treatment. This may be related to the variability in needle weight and needle length. The only significant treatment response in these parameters was a quadratic response for dry weight per cm length of needle. The control, low-N, and high-N treatments had 7.8, 9.3, and 8.4 mg/cm needle length, respectively.

There were significant time effects for needle dry weight, needle N content, and N content per cm needle (Table 8). The needles lost weight and N until August, but increased again in the autumn and winter (Figures 12 through 14). The dry weight/cm needle did not change with time (Table 8 and Figure 15).

There was a significant increase in ^{15}N levels in the needles due to N treatment (Table 8). However, the high-N treatment absorbed about five times the amount of ^{15}N than the low-N treatment, which suggests that uptake into this foliage is not in direct proportion to the amount applied.

The changes in ^{15}N levels in the 1968 needles did not show significant changes with time. As the pretreatment sampling was not included in these statistical analyses, it can be concluded that there were no changes of ^{15}N after the 6th week.

The P in the needles, whether expressed on a concentration

or content basis, did not differ with treatment. The P concentration showed a significant change with time (Figure 16). However, the total P content per needle, or per cm needle did not differ significantly with time (Table 8 and Figures 17, 18).

The Al concentration and P to Al ratio remained unchanged with time (Figures 19, 20). The P to Al ratio had a significant quadratic response to N treatment, the ratio averaging 2.5, 1.7, and 2.2 in the control, low-N, and high-N plots respectively.

Foliage Initiated in 1969

The 1969 foliage was expanding rapidly at the beginning of the experiment. It was sampled over two growing seasons and by the time of final harvest, most had been shed. Because of the long time span involved all measured parameters show significant changes with time (Table 8).

Needle weight was not influenced by treatment. It increased rapidly during the first growing season with accretions continuing into the winter (Figure 14). However, a decline in mean needle weight from 200 mg to 165 mg occurred the following summer. There was an increase again during the second winter, the mean needle weight being about 215 mg at the final sampling date. Similar changes were noticeable in needle data expressed as weight per cm needle (Figure 15).

The N content of the needles followed a similar seasonal

pattern to dry weight; a steady increase until mid-winter followed by a decrease in the summer and an increase again the second winter (Figure 12). In contrast, the mean N concentration decreased from 0.89 to 0.84 percent during the first summer, but increased to 0.95 percent in the winter. In the second summer after foliage initiation there was a gradual decrease in N concentration to 0.63 percent. There was a small rise the following winter (Figure 11).

The N concentration and content of N per needle or per cm needle length were significantly increased by N treatment. The N concentration had significant linear and quadratic components. The mean N concentrations were 0.82, 0.79, and 0.88 percent in the foliage from the control, low-N, and high-N plots. The quadratic treatment effects were not significant for N content data. Thus, the mean N content in samples from the control, low-N, and high-N treatments were 1.19, 1.34, and 1.58 mg.

The P concentration decreased during the summer months from 0.125 to 0.100 percent. After this initial drop there was a general, but erratic, increase in P concentration until needle fall (Figure 16). The P content per needle increased until about the middle of the second summer, after which a slight decrease was observed (Figure 17). An increase in P content per needle was apparent the second winter. The significant quadratic response of P concentration to N treatment did not appear to be important. The mean P concentration in the control, low-N, and high-N treatments were 0.119, 0.108, and 0.119 percent.

The Al concentration increased as the foliage aged (Figure 19). The P to Al ratio decreased rapidly during the summer months and stabilized at about 2.5 to 1 (Figure 20).

The level of ^{15}N expressed as atom percent and percent N from the fertilizer reached a maximum at about 12 weeks after fertilization (Figure 21). At this time some 8.4 and 27.5 percent of the N in the current (1969) needles from the low-N and high-N plots came from the fertilizer. While the maximum occurred at 12 weeks, most of the uptake (expressed in these units) had occurred by six weeks. The maximum uptake expressed on a per needle basis was during March of the year following fertilization, after which the amount of ^{15}N in the needles declined (Figure 22). At needle-fall these needles contained about 50 percent of the ^{15}N they had at their peak content.

Foliage Initiated in 1970

The 1970 needles were initiated in the spring of the year after fertilization. These needles were first sampled in June and were the main needles on the trees at harvest in December 1970.

All parameters showed significant changes with time (Table 8). The dry weight and N and P contents of the needles increased rapidly. By December 1970, the average needle was 151 mg dry weight and contained 1.64 and 0.20 mg of N and P, respectively (Figures 12, 14, 17). The N and P

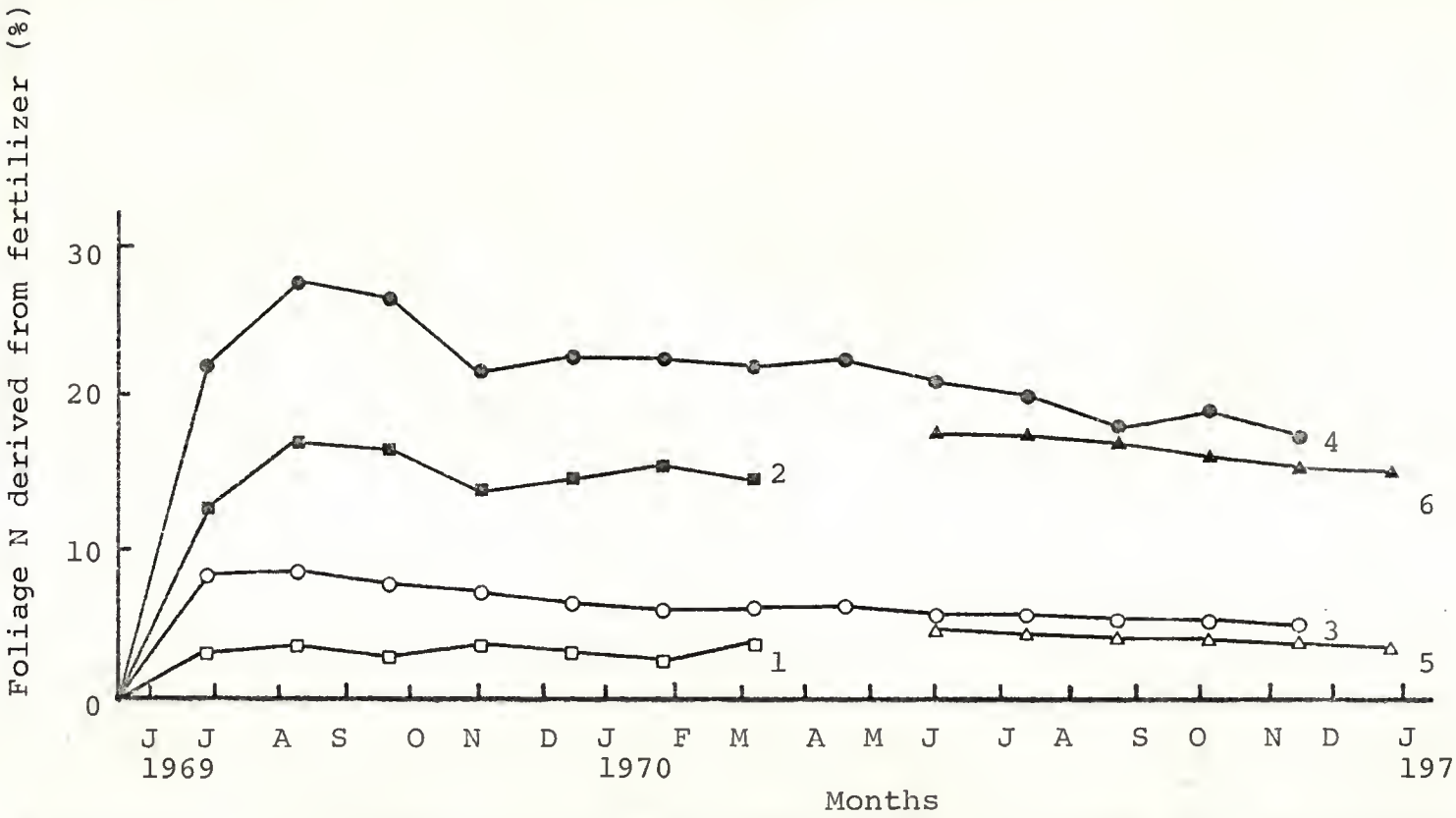

Figure 21. The changes in the percentage of foliage N that was derived from the fertilizer, over two growing seasons. 1 and 2 are low- and high-N treatments for the 1968 foliage; 3 and 4 are low- and high-N treatments for the 1969 foliage; 5 and 6 are low- and high-N treatments for the 1970 foliage.

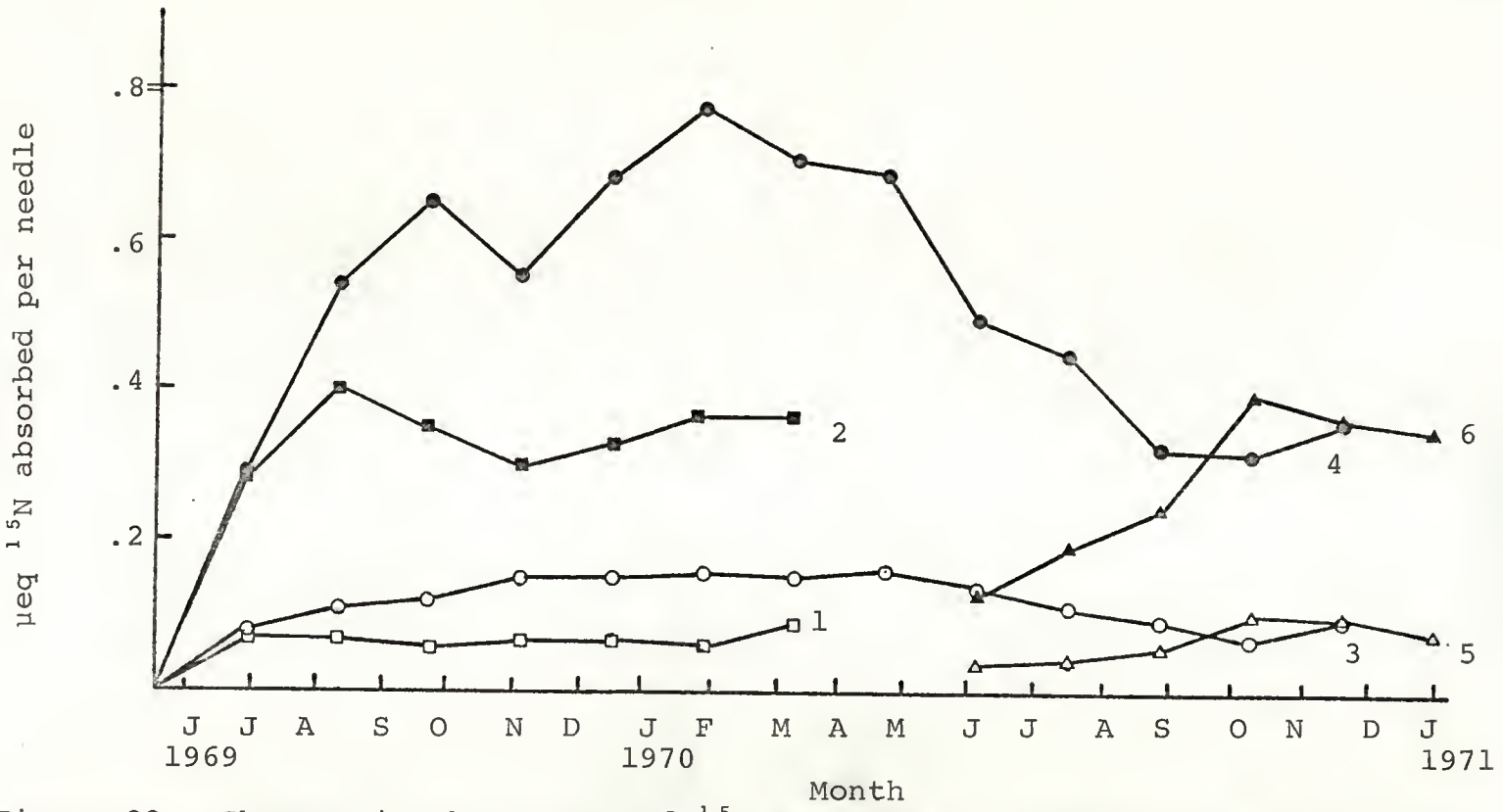

Figure 22. Changes in the amount of ^{15}N absorbed per needle over two growing seasons. 1 and 2 are the low- and high-N treatments for the 1968 foliage; 3 and 4 are the low- and high-N treatments for the 1969 foliage; 5 and 6 are the low- and high-N treatments for the 1970 foliage.

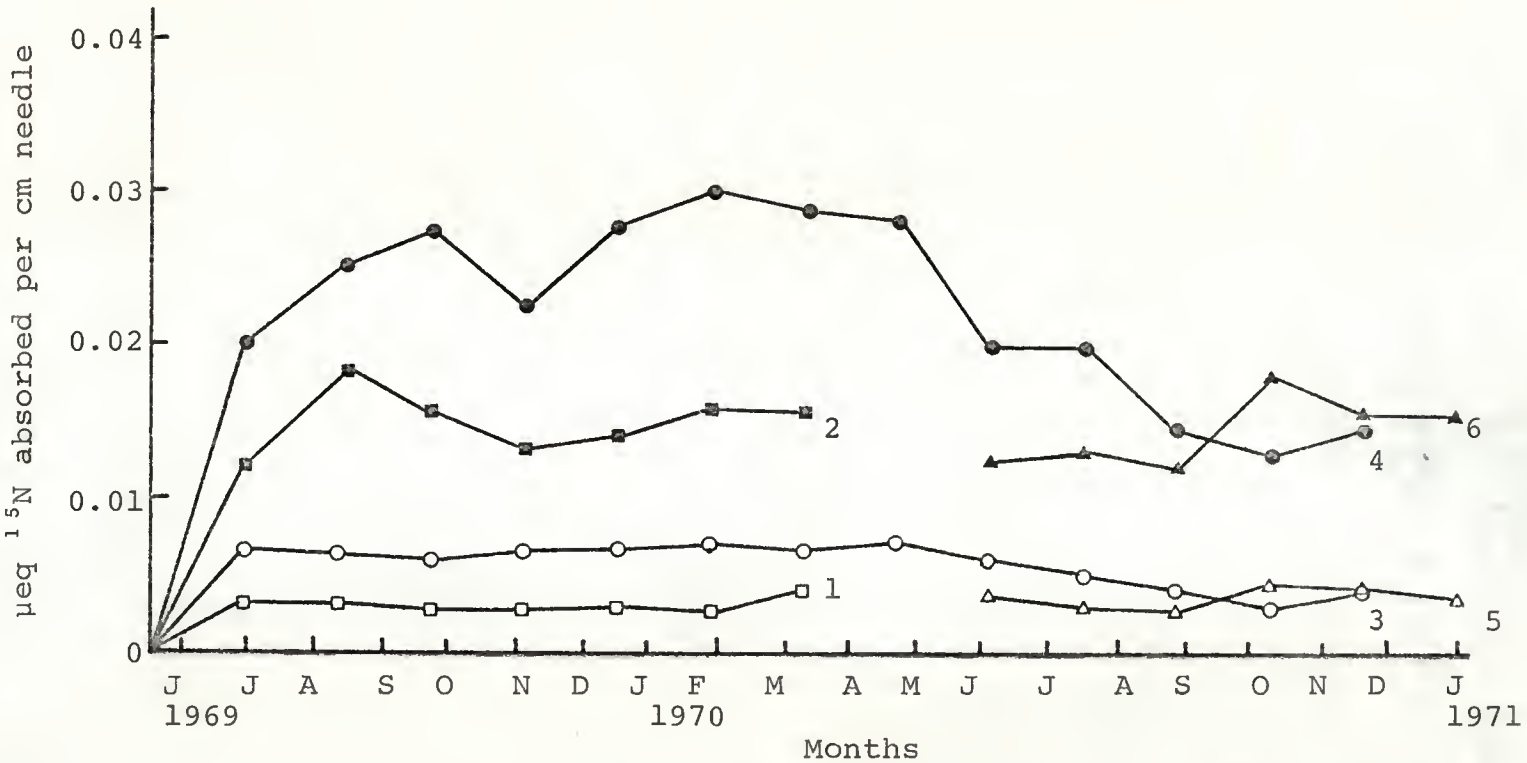

Figure 23. The changes in the amount of ^{15}N absorbed per cm needle over two growing seasons. 1 and 2 are low- and high-N treatments in the 1968 foliage; 3 and 4 are low- and high-N treatments in the 1969 foliage; 5 and 6 are low-and high-N treatments in the 1970 foliage.

concentrations decreased during the summer, but increased again in the autumn (Figures 11, 16). The Al concentration increased from 210 to 390 ppm between June and December. The P to Al ratio showed a rapid drop with time (Figure 20). This was a result of a drop in P concentration with a corresponding rise in Al concentration.

The percentage of ^{15}N derived from the fertilizer and ^{15}N atom percent decreased significantly with time (Figure 21). The ^{15}N absorbed into the needle increased with time (Figure 22). There was a significant time x treatment interaction which resulted from the ^{15}N increasing more rapidly in the high-N plots than in the low-N plots (Figure 22). The difference between treatments were also highly significant (Table 8).

The ^{15}N absorbed per cm needle showed a gradual significant increase with time, the increase being at a greater rate in the high-N plot (Figure 23).

Comparison Among Foliage Ages

The observations on needle parameters followed distinct patterns from flushing to needle fall. These patterns were studied over two growing seasons for the 1969 flush and over shorter lengths of time for the 1968 and 1970 flushes.

The weight and N content of the current needles increased rapidly during the first summer; reached a peak in late winter; declined the following summer; and tended to rise again in the autumn and winter. The P content of the

needles followed a similar trend, but did not show the marked decrease in the second summer. The dry weight and N and P contents per cm needle length showed less noticeable changes with time, but the patterns were otherwise similar.

The N and P concentrations, when not influenced by N treatment, decreased during the first summer following initiation, and increased again in the winter. Thereafter, the P concentration continued to rise until leaf-fall, whereas N concentrations decreased during the second summer.

The Al concentration in the foliage showed a continual rise from initiation until leaf-fall. The very young foliage had about 200 ppm Al while the oldest foliage often had 600 ppm Al. The P to Al ratio decreased from 6:1 to 2.5:1 in the first summer following initiation and then stabilized at this lower level.

The 1969 foliage, which was rapidly expanding at the time of fertilization, accumulated higher amounts of ^{15}N from the fertilizer than did the older (1968) foliage. The 1969 foliage also had higher ^{15}N atom percent levels than the 1970 foliage at the same time period. The ^{15}N atom percent of the 1970 flush decreased with time. The ^{15}N content of the 1970 needles increased with time and eventually surpassed the ^{15}N content of the 1969 needles (Figure 22).

The comparison of needles per fascicle in the 1969 and 1970 foliage did not reveal any influence of N treatment on this character.

Movement of N in the Soil

The ammonium sulphate was applied in granular form to the litter layer. Because of delequesience the granules had dissolved by the following afternoon even though no rain was recorded. The amount of labelled N remaining in the litter layer decreased rapidly with time (Figure 24). The indications are that the N was leached rapidly through the litter. By the end of the third week about 20 and 16 percent of the N applied to the low-N and high-N plots remained. By 6 weeks the high-N plots had only 9 percent remaining in the litter; the low-N plots were unchanged. The amount of N in the litter decreased slowly after this initial drop. In terms of absolute amounts of fertilizer-N held in the litter, the retention at 6 weeks was equal to 38 and 68 meq/kg litter for the low- and high-N plots, respectively. Thus, considerably more N was held in the litter of the high-N plots, but not in proportion to the amount applied.

The movement down the soil profile is illustrated by Figures 25 and 26 and Appendix D, Table 27. At all sampling dates the majority of labelled N in the mineral soil was in the surface 10 cm.

The depletion of fertilizer-N from the soil (including the litter), over the 84 weeks is illustrated in Figure 27. There was a rapid decline during the first 12 weeks. The rate of depletion was slower after this date. As with the litter alone, the decline was greater for the high-N plots

when expressed as a percent of applied N, but in terms of absolute amounts considerably more remained. After 6 weeks 62 and 50 percent of the low- and high-N rates respectively could be accounted for in the soil. The percentages had dropped to 39 and 22 percent at 12 weeks and to 28 and 17 percent at 84 weeks. The first 3 months are thus the most important in the depletion of fertilizer-N from this soil system.

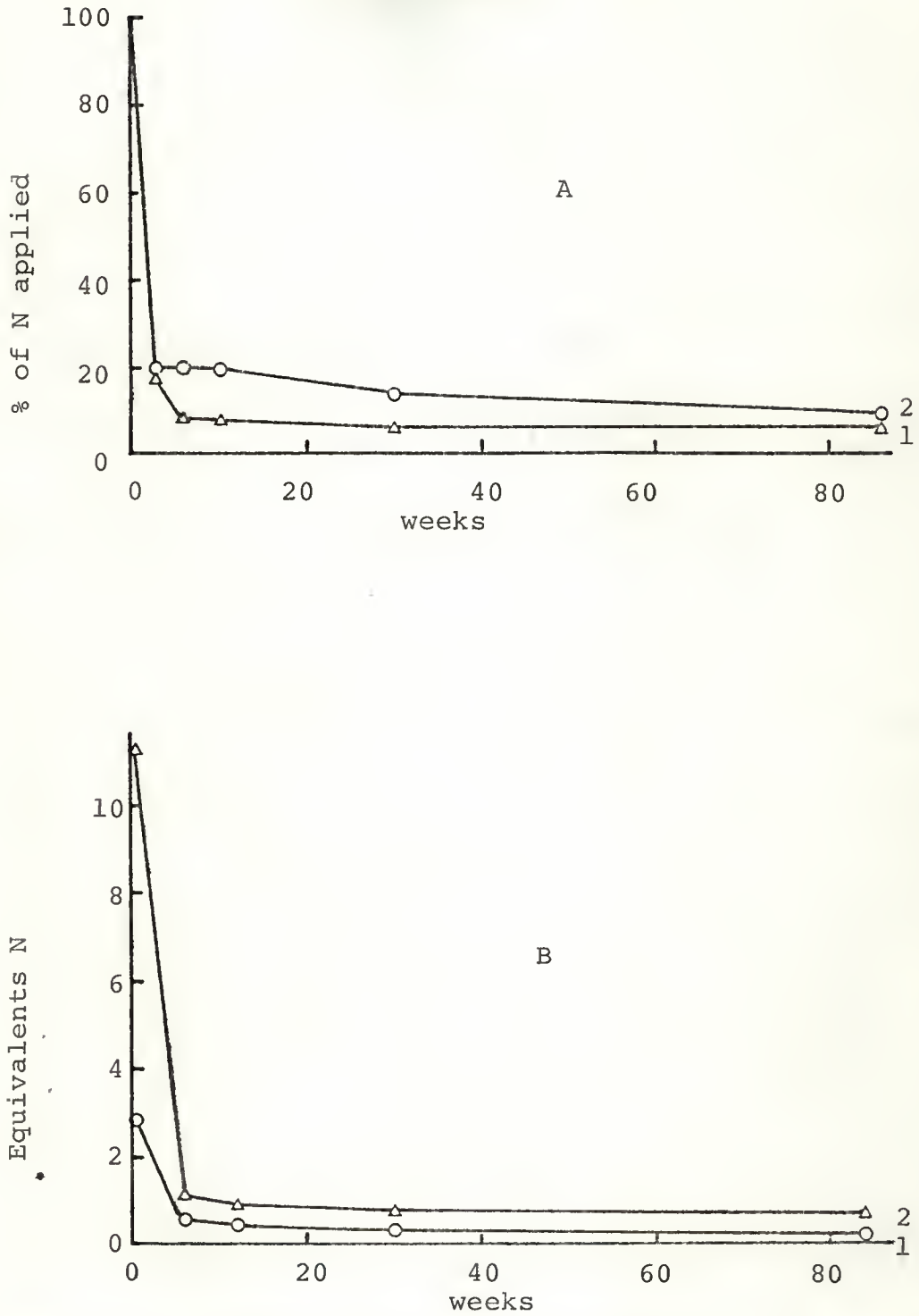

Figure 24. Changes in the amount of applied N in the litter during the 84 weeks following fertilization; A--as a percentage of the amount applied; B--as equivalents of N remaining. 1 and 2 are low- and high-N treatments, respectively.

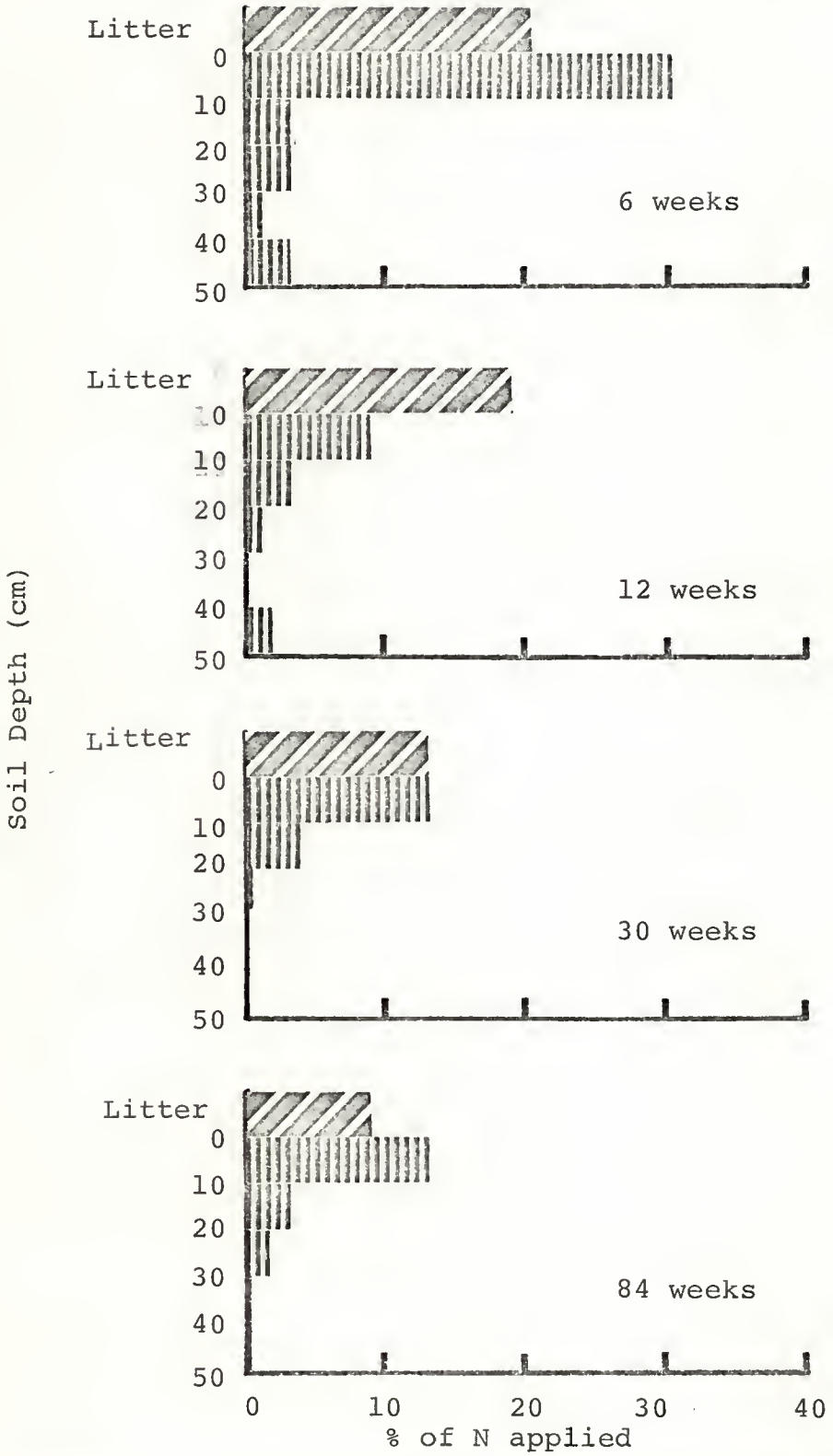

Figure 25. The distribution of applied N in the litter and soil of the low-N treated plots at 6, 12, 30, and 84 weeks after fertilization.

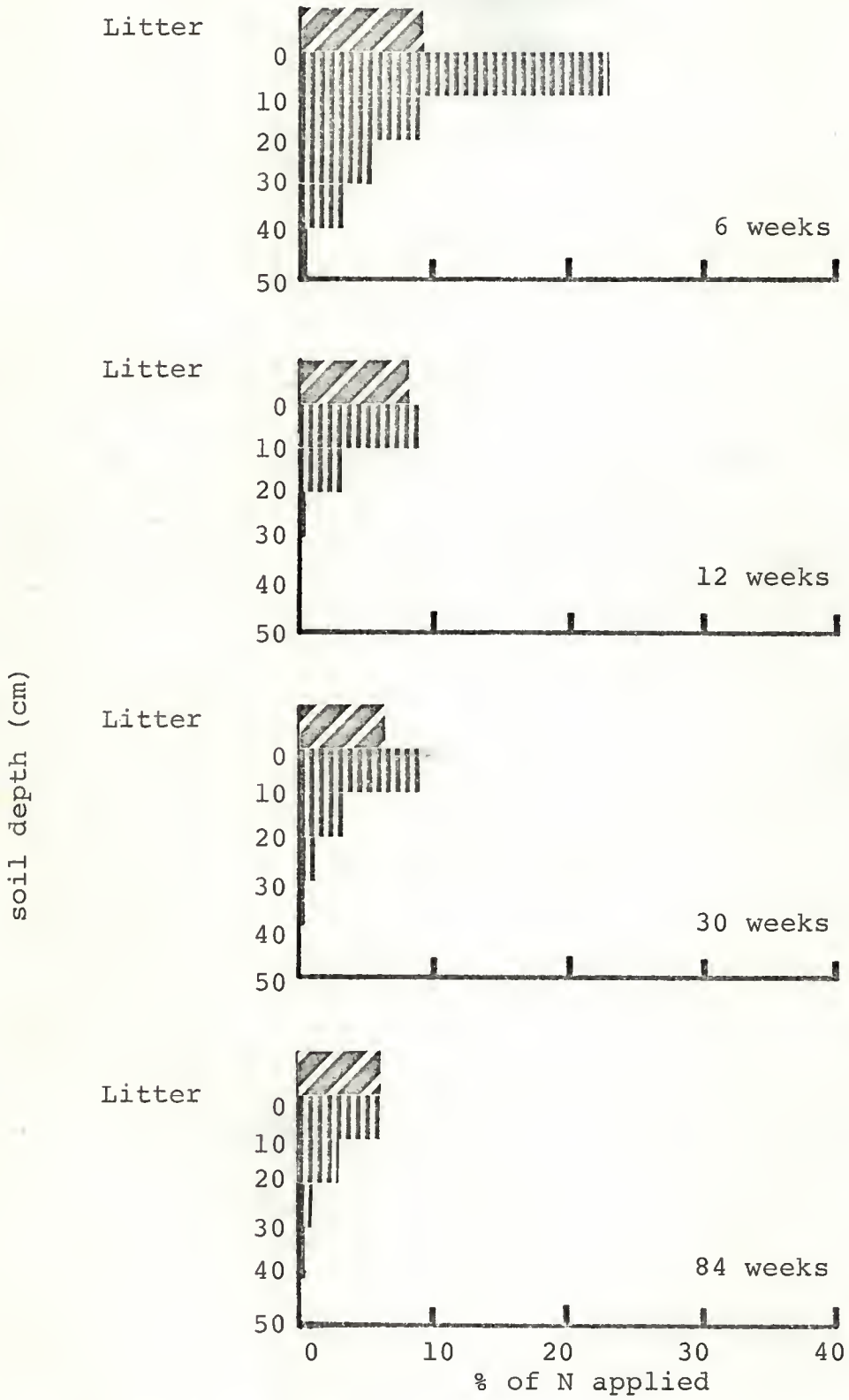

Figure 26. The distribution of applied N in the litter and soil of the high-N treated plots at 6, 12, 30, and 84 weeks after fertilization.

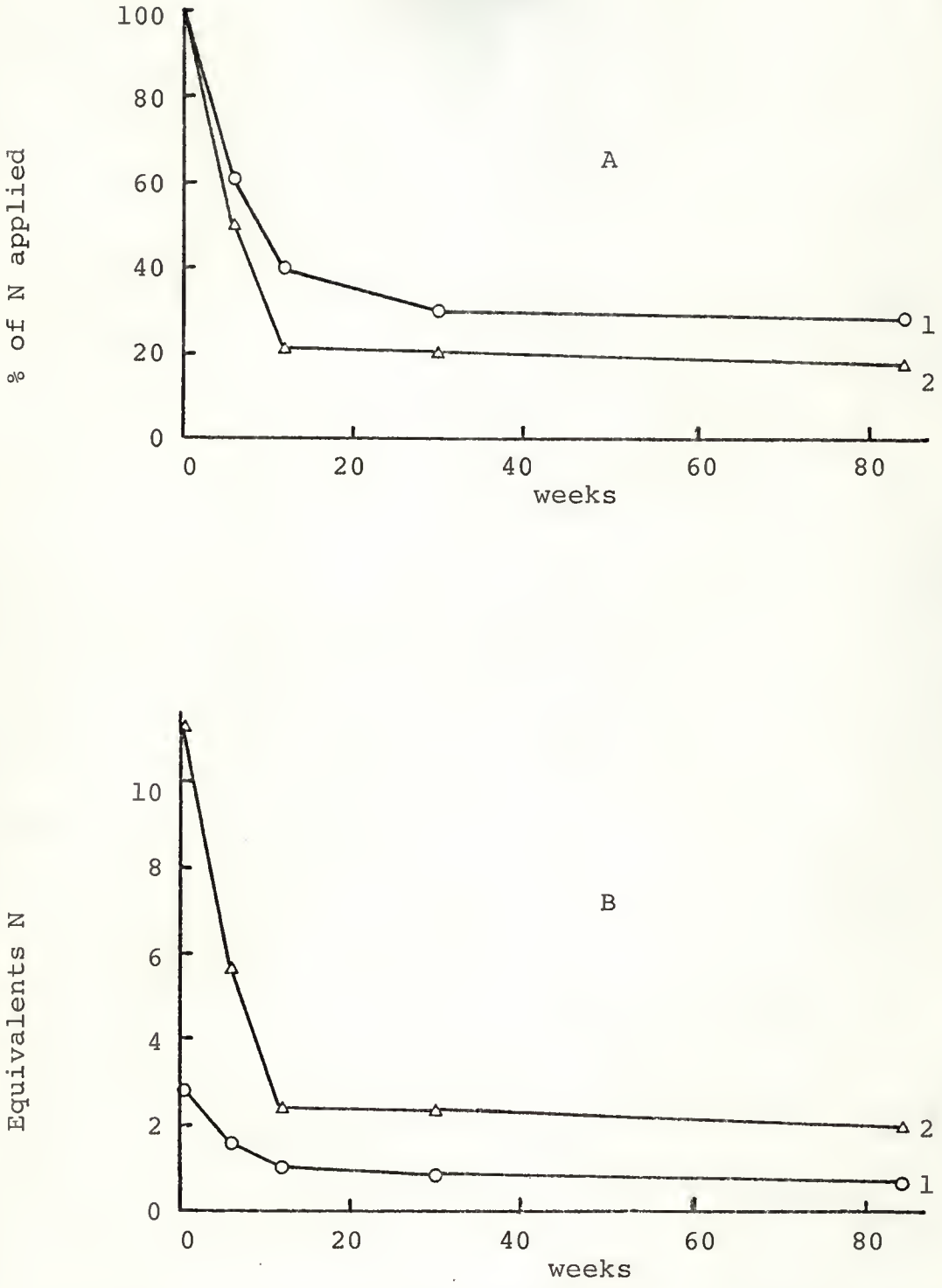

Figure 27. Changes in the amount of applied N in the litter and soil during the 84 weeks following fertilization; A--as a percentage of the amount applied; B--as equivalents of applied N remaining. 1 and 2 are low- and high-N treatments respectively.

Destructive Sampling at 19 Months

Sample Trees

The dry weight, N concentration, ^{15}N atom percent, total N, and ^{15}N contents for the components of each tree are given in Appendix E, Table 52 and are summarized by fertilizer treatments in Tables 9 and 10.

The trees had shed the major portion of their 1969 foliage, for at harvesting only 7 percent of the foliage weight was in this age group. The largest portion of the biomass (52 percent) occurred as stem wood. Bark accounted for another 15 percent and roots 21 percent. The crown was evenly divided between branchwood and foliage, each of these making up 6 percent of the dry weight. There was no significant effect of N treatment on any component except for fine taproots which were more prolific in the high-N treated trees (Table 11).

The distribution of total N and N derived from the fertilizer were quite different from biomass or from each other. Some 29, 25, 21, 16, and 9 percent of the total N occurred in foliage, stem-wood, roots, bark, and branches, respectively. Of N derived from the fertilizer, 41 percent was found in the foliage; the stem-wood, roots, bark, and branches had 22, 15, 9, and 13 percent, respectively.

Except for fine taproots, the analysis of variance for N content in the tree components did not show significant responses due to N treatments (Table 11).

Table 9. Biomass and total N in the trees as influenced by N treatment.

Component	Control		56 kg N/ha		224 kg N/ha	
	Dry weight	Total N	Dry weight	Total N	Dry weight	Total N
	g					
Foliage-1970	4,310	40.2	4,940	44.0	4,350	37.8
Foliage-1969	290	2.1	390	2.8	310	2.3
Total foliage	4,600	42.3	5,330	46.8	4,660	40.1
Branches-69-70[a]	2,100	6.3	2,520	8.0	2,160	7.0
Branches-pre-69	3,020	5.0	4,300	7.6	2,820	5.1
Branches-dead	2,740	4.6	2,540	4.0	1,950	3.2
Total branches[b]	5,120	11.3	6,820	15.6	4,780	12.1
Stem-bark	13,450	23.6	13,010	23.4	12,610	22.6
Stem-wood	43,150	33.4	50,730	38.2	42,170	39.9
Roots-fine laterals	1,220	6.2	990	4.2	880	4.4
Roots-large laterals	5,100	10.4	5,200	11.2	4,430	11.4
Roots-fine tap	80	0.3	70	0.2	170	0.6
Roots-large tap	11,210	13.5	14,110	16.3	12,220	17.0
Total roots	17,610	30.4	20,370	31.9	17,700	33.4
Total tree[b]	83,930	141.0	96,260	155.9	81,920	148.1

[a] Includes buds.

[b] Excludes dead branches.

Table 10. Labelled N in the trees at harvesting as influenced by fertilizer rate.

		56 kg N/ha		224 kg N/ha	
		^{15}N atom %	N from fertilizer meq	^{15}N atom %	N from fertilizer meq
Foliage	1970	0.443	117.3	0.704	447.0
	1969	0.434	8.0	0.701	28.7
Total foliage			125.3		475.7
Branches	1969-70	.439	19.3	0.688	74.8
	pre-1969	.429	16.2	0.648	48.0
	Dead	.403	5.0	0.525	17.6
Total branches[a]			35.5		122.8
Buds		0.443	1.4	0.701	6.1
Stem - Bark		0.401	25.1	0.513	114.0
Stem - Wood	1969-70	0.450	31.6	0.669	118.6
	Wood pre-1969	0.401	32.1	0.501	138.8
Total Stem			88.8		371.4
Roots	Inner fine	0.462	4.7	0.619	18.2
	Inner large	0.424	14.9	0.598	66.2
	Outer fine	0.384	1.7	0.448	7.0
	Outer Large	0.391	3.3	0.476	12.4
	Tap fine	0.405	0.3	0.500	3.0
	Tap large	0.405	5.4	0.515	24.2
	Stump	0.396	12.0	0.499	57.1
Total root			42.3		188.1
Total Tree[b]			298.3		1181.7

[a] Total of live branches only.

[b] This total includes dead branches.

Table 11. Summary of analyses of variances of the effect of fertilizer treatment on dry weight and total N in various components of the trees.

Component	Dry weight	Total N
	F[a]	
Foliage - 1970	0.56	0.53
Foliage - 1969	0.14	0.11
Bark	0.61	0.23
Wood	3.26	0.75
Branches-1969-70[b]	0.57	0.91
Branches-pre-1969	1.48	1.77
Roots-fine laterals	0.29	0.36
Roots-large laterals	0.53	0.09
Roots-fine tap	5.45*	5.85*
Roots-large tap	2.91	0.67

* Significant at 5 percent level.

[a] Three treatments, four replications in a completely randomized design.

[b] Includes buds.

Table 12. Summary of the analysis of variance of N concentration and ^{15}N atom percent in various parts of the tree at harvesting.

Source	1970 Foliage		Branches		Stem	Roots	
	% N	^{15}N atom %	% N	^{15}N atom %	^{15}N atom %	% N	^{15}N atom %
	significance level						
Treatment (A)	ns	***	ns	***	***	ns	***
Component (B)	ns	***	**	***	***	***	***
A x B	ns	ns	ns	***	***	ns	***

ns Not significant at 5 percent level.

** Significant at 1 percent level.

*** Significant at 0.1 percent level.

Similarly, the analysis of N concentration in 1970 foliage, roots, and branches did not indicate significant treatment responses (Table 12). Components within each of these groups were treated as 'sub-plots' in a split-plot analysis of variance. Details of the analyses are given in Appendix E. There were significant differences in N concentration between types of branches and between root subdivisions. However, the N concentration in the 1970 foliage did not differ with crown level (Table 12).

The ^{15}N atom percent in the 1970 foliage, branches, stem, and roots were also statistically analysed using the same split-plot model (Appendix E and Table 12). With these analyses the control treatment is omitted and the treatment comparison is between high-N and low-N treatments. The ^{15}N atom percent in the 1970 foliage was significantly higher in the high-N plot. The sum of squares for crown level was partitioned into two single degree of freedom contrasts; one to compare terminal foliage with upper and lower crown foliage; the second to compare upper crown with lower crown. The tests showed that, at a significance level of 5 percent probability, the ^{15}N atom percent of the terminal foliage was significantly higher than foliage in other parts of the crown, and that the ^{15}N atom percent in the upper and lower crown foliage did not differ.

The ^{15}N atom percent in the branches were significantly higher in the high-N than in the low-N treatment (Tables 10, 12). The branch components and the interaction of branch

components x treatments were also significant. To determine which components were significantly different, Tukey's honestly significant difference (hsd) test was applied to components within each treatment (Steel and Torrie, 1960). The significance level of 5 percent probability was used. This analysis showed that the ^{15}N atom percent in the categories of living branches, from the low-N treated trees, were not significantly different. All live 1969-70 branchwood had significantly higher ^{15}N atom percent than the dead branches. The lower crown pre-1969 branches did not differ significantly in ^{15}N atom percent from the dead branches. Upper crown pre-1969 branches were excluded from the analysis as often they were not present in the tree. With the high-N treatment the only groups of branches not differing significantly from one another were the 1969-70 branches from the upper and lower crown. The levels of ^{15}N atom percent in the branches of trees from the high-N plots were 0.694, 0.683, 0.640, and 0.525 for the upper crown 1969-70, lower crown 1969-70, lower crown pre-1979, and dead branches, respectively.

The ^{15}N atom percent in the roots was significantly increased by N treatment (Table 12). The component and treatment x component interactions were also significantly different so Tukey's hsd test was used to determine which components within each treatment, differed in their ^{15}N atom percent. In the low-N treatment, inner fine lateral roots were significantly higher than other types of roots,

except for the inner large roots. No other significant differences were found. In the high-N treated trees the inner fine and inner large laterals again were not different in ^{15}N atom percent, but both were significantly higher than other roots. The taproots, stump, and outer large roots were not different. The taproots and stumps differed from the outer fine roots, but the outer large and outer fine laterals did not differ significantly. In summary, inner laterals tended to be higher in ^{15}N than other roots and outer fine roots tended to have the lowest levels.

The ^{15}N atom percent in the stem showed a significant increase due to N treatment. The components of the stem (bark, 1969-70 wood and pre-1969 wood) and the component x treatment interaction were also significant (Table 12). The bark, 1969-70 wood, and pre-1969 wood for the low-N treatment had 0.401, 0.450, and 0.401 ^{15}N atom percent, and for the high-N treatment had 0.513, 0.669, and 0.501 ^{15}N atom percent respectively. The bark and pre-1969 wood are lower than the 1969-70 wood. The latter was formed after fertilization.

The amount of N derived from the fertilizer by the various components generally showed significant increase to treatment (Table 13). The 1969 foliage, pre-1969 branches, fine roots and stumps were exceptions, probably as their dry weights were so variable. The overall recovery of fertilizer N in the trees showed a highly significant linear relationship to treatment (Figure 28). The linear

Table 13. Summary of analysis of variances of the amount of N derived from the fertilizer in various components of the tree, as measured by the use of tagged N.

Component		F[a]	
Foliage	1970	33.96	**
	1969	1.03	
Branches	1969-70	17.31	**
	pre-1969	5.04	
	Dead	8.21	*
Buds		21.25	**
Bark		49.30	***
Wood	1969-70	23.66	**
	pre-1969	614.29	***
Roots	Inner fine	4.11	
	Inner large	14.95	**
	Outer fine	5.48	
	Outer large	10.07	*
	Tap fine	10.97	*
	Tap large	11.46	*
	Stump	5.20	

[a] Two treatments, four replications in a completely randomized design.
* Significant at 5 percent level.
** Significant at 1 percent level.
*** Significant at 0.1 percent level.

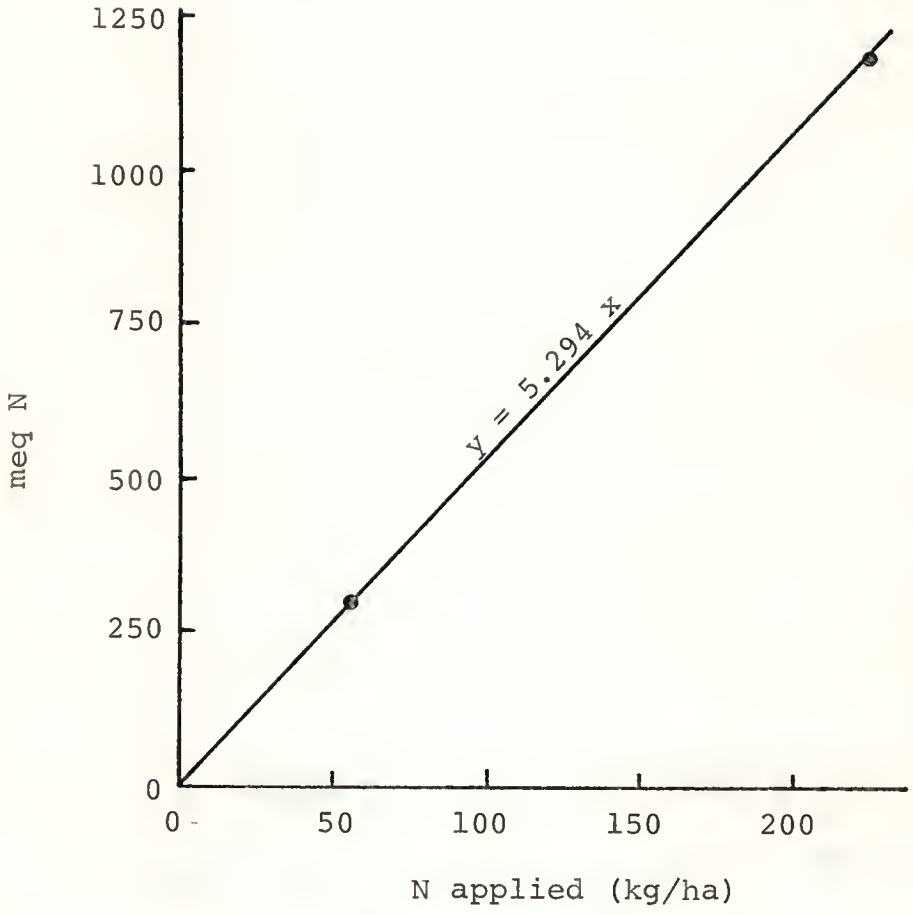

Figure 28. The amount of N from the fertilizer in the trees at the end of the second growing season. Points are averages of four replications.

regression of N uptake against fertilizer rate passes through the origin. The inclusion of the constant, a, in the equation:

$$y = a + bx$$

did not improve the fit. The correlation coefficient with or without 'a' is r = 0.921.

The recovery of added fertilizer in the trees expressed on the basis of percentage of N applied is summarized in Table 14. An average of 10.5 percent of the applied N was recovered in the trees. The percentage ranged from 7 to 15 percent. Recovery was the same for both high- and low-N treatments.

Ground Vegetation

Ground vegetation was generally sparce and varied considerably in dry weight between plots. The dry weight, N concentration, ^{15}N atom percent, N uptake from the fertilizer, and percent N recovery are summarized in Table 15. The ground vegetation accounted for a very small fraction of the applied nitrogen. The analysis of variance of N concentration and ^{15}N atom percent in the ground vegetation is given in Appendix E, Table 57.

Litter

The mean dry weight of all 24 litter samples collected at harvesting was equivalent to 21,160 kg/ha. There was no difference in litter dry weight due to N treatment (Table 16

Table 14. Recovery of added N fertilizer in trees after two growing seasons.

Treatment	Plot	Foliage	Branches and buds	Stem	Total above-ground	Roots	Grand total
		%					
Low-N	5	6.86	2.21	4.12	13.19	1.80	14.99
	6	3.73	1.42	2.88	8.03	1.84	9.87
	7	2.77	0.95	2.07	5.79	1.22	7.01
	8	4.37	1.34	3.50	9.21	1.13	10.34
	Mean	4.43	1.48	3.14	9.05	1.50	10.55
High-N	9	2.72	0.66	2.63	6.01	1.17	7.18
	10	4.26	1.30	3.54	9.10	1.55	10.65
	11	4.32	1.28	3.47	9.07	1.46	10.53
	12	5.54	1.94	3.50	10.98	2.60	13.58
	Mean	4.21	1.30	3.28	8.79	1.70	10.49

Table 15. Dry weight and N in the ground vegetation, as influenced by N fertilizer treatment.

N applied	Distance from tree	Dry weight	N	^{15}N	N from fertilizer	N recovered
kg/ha	m	g	%	atom %	meq	%
0	0-1½	238	0.84	-	-	-
0	1½-2½	316	0.89	-	-	-
56	0-1½	41	0.84	0.467	1.1	0.04
56	1½-2½	242	0.78	0.396	1.9	0.07
224	0-1½[a]	24	0.65	0.794	2.3	0.02
224	1½-2½	67	0.72	0.428	1.1	0.01

[a] One plot had no ground vegetation.

Table 16. A summary of the dry weight, N and ^{15}N levels in the litter samples collected from plots at harvesting, as influenced by N treatment.

Treatment	Dry weight	N	N	^{15}N	Fertilizer N per plot	N recovered
	kg/ha	%	kg/ha	atom %	meq	%
No N	19,420	0.494	95	0.367	-	-
56 kg N/ha	21,780	0.525	114	0.455	255	9.0
224 kg N/ha	22,280	0.582	131	0.579	697	6.2

and Appendix E, Table 58). The concentration of N in the litter increased significantly with treatment. Litter from control plots had 0.494 percent N, compared to 0.525 and 0.582 percent in the low- and high-N plots. However, the total N contents of the litter were not significantly different due to treatment.

The ^{15}N atom percent in the litter was significantly higher in the high-N plots when compared to the low-N plots (Table 16, and Appendix E, Table 58). Similarly the meq of fertilizer-N, remaining in the litter of the plots, differed significantly between the two treatments. Although the mean percentage of N recovered in the litter was 9.0 and 6.2 percent for the low- and high-N plots respectively, this difference was not significant. The variation between plots was considerable.

Soils

The details of the total N and labelled N found in the soil under each tree at harvesting is given in Appendix E, Table 59. The N concentration decreased significantly with depth (to 50 cm) but did not show an increase to the added N. The top 10 cm of mineral soil had a mean N concentration of 0.04 percent. This decreased to 0.02 percent at 50 cm. Below the A_1 horizon (i.e., below 60 cm) the N concentration was very low, being consistently below 0.01 percent. It increased slightly in the B_2h horizon.

The ^{15}N atom percent was significantly higher in soils

from plots treated with the heavy application of N, compared to those receiving the low rate (Table 17). There was also a significant decrease in ^{15}N with depth, and a significant depth x treatment interaction. The interaction is illustrated in Figure 29. This figure also illustrates the leaching of the fertilizer-N down the profile and the higher retention of ^{15}N in the upper portion of the A_1 horizon.

There was more fertilizer-N recovered from the low-N plots when the results were expressed as a percentage of the amount applied. The average recovery from the soil to a depth of 2 m was 20.6 percent for the low-N plots and 11.7 percent for the high-N plots (Table 18). The amount recovered below 50 cm depth was very small (2.0 and 0.7 percent for the low- and high-N plots, respectively).

Surrounding Trees

The equation relating tree diameter to foliage biomass is

$$\log \text{foliage dry wt} = 0.5325 + 2.6208 \log \text{dbh}$$

$$r = 0.96$$

This equation was used to obtain the foliage dry weight of trees immediately surrounding each plot (Table 19). By combining weight data and ^{15}N atom percent, the total uptake into the foliage of the surrounding trees was calculated (Table 19). In the 12 sample trees, foliage uptake accounted for 41 percent of total ^{15}N absorbed by the trees. To

Table 17. Analyses of variances of N concentration and ^{15}N atom percent in the soil at harvesting.

Source	df	% N		^{15}N atom %	
		ms x 10^{-7}	F	ms x 10^{-7}	F
Treatment (A)	1	96	0.35	19,460	61.57***
Error (a)	6	270		316	
Soil Depth (B)	4	5,096	31.23***	20,790	75.83***
A x B	4	328	2.01	3,138	11.45***
Error (b)	24	163		274	

*** Significant at 0.1 percent level.

Table 18. Recovery of added N fertilizer in ecosystem after two growing seasons.

Treatment	Plot	Sample trees	Soil[a]	Litter	Ground vegetation	Surrounding trees	Total
		%					
Low-N	5	15.0	22.1	5.3	0.1	13.0	55.5
	6	9.9	22.5	10.2	0.2	10.4	52.8
	7	7.0	26.8	10.9	0.1	19.5	64.3
	8	10.3	10.8	9.7	0.1	13.3	44.2
	Mean	10.6	20.6	9.0	0.1	14.0	54.2
High-N	9	7.2	9.2	4.4	0.0	22.4	43.2
	10	10.7	12.6	6.4	0.0	12.2	41.9
	11	10.5	11.9	7.2	0.1	14.0	43.7
	12	13.6	13.2	6.6	0.0	15.9	49.3
	Mean	10.5	11.7	6.2	0.0	16.1	44.5

[a] Sampled to a depth of 2 m.

Table 19. Estimated foliage dry weight and fertilizer-nitrogen uptake by trees surrounding the sample plots.

Treatment	Plot number	Foliage dry weight[a]	N	^{15}N[b]	Recovery in foliage	Total recovery[c]
		kg	%	atom %	%	
54 kg N/ha	5	35.9	0.905	0.378	5.3	13.0
	6	35.0	0.880	0.376	4.2	10.4
	7	58.0	0.912	0.377	7.9	19.5
	8	43.6	0.905	0.376	5.4	13.3
224 kg N/ha	9	55.1	0.884	0.425	9.1	22.4
	10	26.6	0.908	0.431	5.0	12.2
	11	39.1	0.862	0.419	5.7	14.0
	12	55.7	0.831	0.410	6.5	15.9

[a] Estimated using an equation relating dry weight of foliage and tree diameter.

[b] The ^{15}N atom percent in untreated trees was 0.365.

[c] Total recovery is calculated by assuming that the foliage represented 41 percent of total tree uptake.

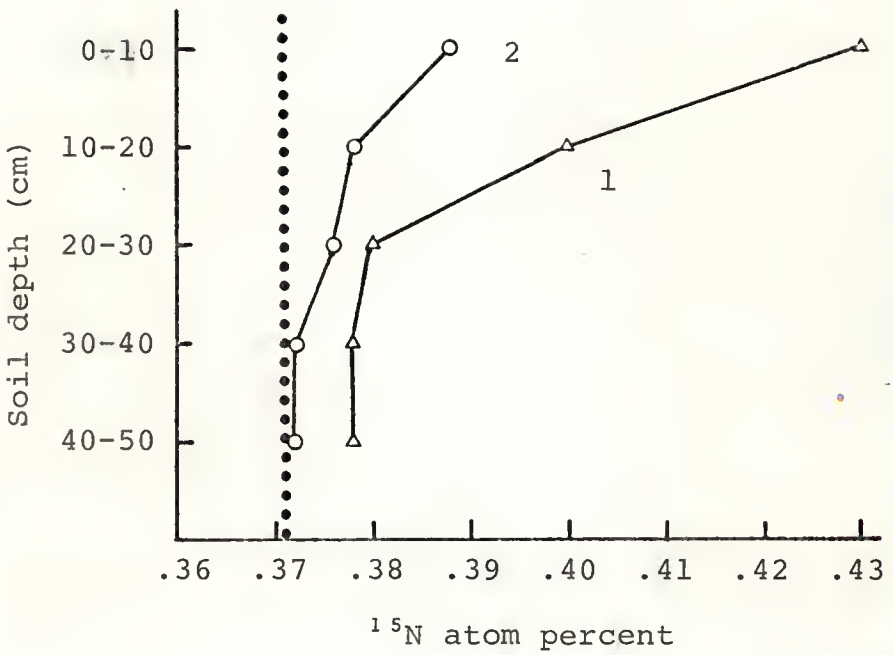

Figure 29. The ^{15}N atom percent in the soil N, 84 weeks after fertilization with ammonium sulphate, as influenced by soil depth and rate of fertilizer application. Dotted line represents normal ^{15}N enrichment in the soil. 1 and 2 are high- and low-N treatments, respectively.

calculate total uptake of fertilizer by the surrounding trees, it was assumed that uptake into their foliage was also 41 percent of their total uptake. The uptake by surrounding trees, expressed as a percentage of applied N, averaged 15 percent (Table 18).

Recovery in Ecosystem

The total recovery of labelled N in the ecosystem at harvesting was about 50 percent. The high- and low-N treatments did not differ significantly (Table 18). About 10 percent of the applied N was recovered from the sample trees and another 15 percent from surrounding trees. The remainder was recovered from the litter and soil (Table 18).

Supplementary Studies

Tree Measurements and Growth

The detailed mensurational data on the sample trees are given in Appendix F, Table 60. At harvesting the trees averaged 13.9 m height, 15.7 cm diameter, with an average crown radius of 1.9 m. The height increment over the two growing seasons of the experiment was 1.9 m. The mean volume increment was 9.9 dm^3/year. The height to the long-term sampling whorl averaged 9.9 m.

Height increment, volume increment, basal area breast-height increment, and cross section area increment at a point 6.5 m above groundline, were analyzed by covariate analysis (Appendix F). The covariates included crown area and the appropriate pretreatment measurement. For basal area increment at 6.5 m the single covariate of crown area was used. In all cases no treatment response was detected.

Rainfall

The raingauge at the Beef Research Unit recorded 68 mm of precipitation 7 weeks prior to the start of the experiment. This occurred during three short wet periods. Two days prior to fertilization, 6 mm of rainfall was recorded. The area was considered to be in a dry period prior to the start of the experiment (Figure 1).

In the 10 weeks following fertilization a total of 270 mm of rainfall was recorded at the Beef Research Unit. This occurred on 23 separate days.

Rainfall recorded in five rain collectors under the trees, totaled 245 mm over the same 10 weeks (Table 20). The difference between the recording at the experimental site and at the Beef Research Unit was due to location and canopy retention. The first rain at the experimental site following fertilizer application occurred on the third day (Table 10). However, it was very light (2 mm) and did not wet the litter or soil appreciably. A heavier rainfall (6 mm) occurred on the 7th day. From the 17th day onward rain became more frequent, with some very heavy rains being recorded in the 8th week after fertilization.

Soil pH

A split-split-plot design was used, with fertilizer as the main plots and time and soil depths as sub- and sub-sub-plots. The effects of fertilizer treatment, time, soil depth and their interactions were significant except for the fertilizer x depth interaction.

The effect the basal treatment of 90 kg P/ha applied as CSP can be seen by comparing pretreatment pH levels with pH levels on the control plots at later sampling dates (Table 22). Six weeks after fertilization, pH had dropped by 0.4 pH units in the 0-10 cm horizon and by a smaller amount (0.2 pH units) below 10 cm. At 36 and 84 weeks the drop was between 0.2 to 0.3 pH units in all parts of the profile.

The ammonium sulphate fertilizer decreased pH beyond that caused by the superphosphate. The influence of this

Table 20. Rainfall reaching the forest floor at the experimental site.

Days after treatment	Rainfall
	mm
3	2
7	6
17,18	19
20	3
25	8
28,29,30	29
31	9
40,41,42	8
49	3
50-56[ab]	111
57-65[a]	40
66-72[a]	8

[a] Exact days of rainfall not known.

[b] Heaviest rainfall on day 51.

Table 21. Analysis of variance of the change of pH in the soil with time, as influenced by fertilizer treatment and soil depth.

Source	df	ms x 10^{-5}	F
Treatment (A)	2	80,146	18.49***
Error (a)	9	4,335	
Time (C)	3	311,644	82.66***
AC	6	20,493	5.44***
Error (c)	27	3,770	
Soil depth (B)	3	264,158	68.30***
AB	6	6,049	1.56
Error (b)	27	3,867	
BC	9	10,602	7.67***
ABC	18	2,590	1.87*
Error (d)	81	1,383	

* Significant at 5 percent level.

*** Significant at 0.1 percent level.

Table 22. The effect of fertilizer treatment on soil pH, as influenced by soil depth and time after fertilization.

Weeks after application	Soil Depth	Fertilizer treatment: 90 kg P/ha — plot number 1	2	3	4	Mean	90 kg P/ha+56 kg N/ha — plot number 5	6	7	8	Mean	90 kg P/ha+56kgN/ha — plot number 9	10	11	12	Mean
0 (pretreatment)	0-10	4.4	5.1	4.9	4.8	4.8	5.4	5.1	5.1	5.2	5.2	4.6	4.9	4.9	5.1	4.9
	10-20	4.7	5.0	5.3	6.2	5.0	5.2	5.2	5.4	5.2	5.2	4.8	5.3	5.4	5.3	5.2
	20-30	5.0	5.0	5.2	5.6	5.2	5.7	5.3	5.4	5.3	5.4	5.2	5.3	5.3	5.5	5.3
	30-50	5.3	5.1	5.2	5.7	5.3	5.3	5.4	5.5	5.2	5.4	5.6	5.1	5.3	5.3	5.3
6	0-10	4.4	4.6	4.5	4.2	4.4	4.2	4.4	4.1	4.4	4.3	3.8	4.2	3.8	3.9	3.9
	10-20	4.6	4.8	4.9	4.7	4.8	4.2	4.8	4.6	4.6	4.6	3.9	4.2	4.3	4.0	4.1
	20-30	4.9	4.9	5.2	5.1	5.0	4.7	5.0	4.5	4.6	4.7	4.4	4.8	4.6	4.6	4.6
	30-50	5.0	4.9	5.1	5.2	5.0	5.2	5.0	5.0	5.0	5.0	5.0	5.0	5.0	4.8	5.0
36	0-10	4.5	4.6	4.7	4.4	4.6	4.5	4.7	4.6	4.6	4.6	4.0	4.3	4.3	4.1	4.2
	10-20	4.8	4.9	4.9	4.7	4.8	4.8	4.8	4.9	4.9	4.8	4.4	4.7	4.6	4.7	4.6
	20-30	4.9	5.0	5.0	4.9	5.0	4.9	4.7	4.9	4.9	4.8	4.9	4.7	4.8	4.6	4.8
	30-50	4.9	5.0	5.0	5.0	5.0	5.0	4.9	5.1	4.8	5.0	4.7	4.6	4.8	4.6	4.7
84	0-10	4.5	4.7	4.7	4.4	4.6	4.5	4.6	4.6	4.9	6.5	4.3	4.2	4.1	4.4	4.2
	10-20	4.6	4.9	4.7	4.7	4.7	4.6	4.8	4.9	6.7	4.8	4.6	4.4	4.6	4.7	4.6
	20-30	4.9	5.1	5.0	4.9	5.0	4.8	4.9	5.0	4.8	4.9	4.9	4.8	4.7	4.9	4.8
	30-50	5.1	4.9	5.0	5.1	5.0	5.1	4.8	4.9	4.9	4.9	5.0	5.0	4.8	4.9	4.9

fertilizer was most marked in the upper portion of the profile (0-30 cm) at all sampling dates. The effect tended to decrease somewhat with time. Thus, in the 0-30 cm soil depth at six weeks, 56 kg N/ha as ammonium sulphate decreased the pH by 0.5 units more than the CSP. At 36 and 84 weeks the decrease was 0.3 pH units. Similarly the high-N treatment of 224 kg N/ha decreased pH by 0.7 pH units at six weeks and by 0.4 pH units at later sampling dates. As would be expected, with pH being on a logarithmic scale, the effect of applying four times the amount of ammonium sulphate does not lead to a four-fold reduction in pH. The maximum pH reduction came at the six weeks sampling date in plots receiving the high-N rate plus CSP; here pH in the top 20 cm was reduced by about 1.0 pH unit.

The significant fertilizer x time interaction was caused by the different behavior of the fertilizer materials with time. The CSP treatment did not lower the pH as greatly with time as did the N treatments. The depth x time interaction is due to the pH changes being greater in the upper soil horizons. The fertilizer x depth interaction was not significant indicating the fertilizers were similar in their effects of reducing pH in the upper soil. The three-way interaction of time x depth x fertilizer was significant as a result of the combination of effects described above.

Soil Nitrate Levels

The soil nitrate levels in the high-N plots are summarized

in Table 23. The levels are uniformly low, never going above 4 ppm. These data indicate that nitrification in these soils was of minor importance.

Table 23. Nitrate in the soil of the high-N plots, as measured by nitrate-ion electrode.

Soil depth	Pretreatment	Weeks after fertilizer applied 6	12[a]	30	84
cm			NO_3^- ppm[b]		
0-10	3	1-2	1	2-3	1
10-20	1-3	1-3	2	1-2	1
20-30	1-2	2-4	2	1-2	1
30-50	1-2	2	2	1-2	1

[a] Analysed on a single bulked sample for each depth. All other samples analysed on an individual tree basis and range in values are given.

[b] 1 ppm indicates the sample was at or below the lowest standard ie $\leq$ 1.2 ppm $^-NO_3$.

DISCUSSION

Uptake of Isotopes into Foliage

The first indication of the labelled P reaching the tree crowns was 7 days after fertilizer application. The amounts detected at this time were very small, but significantly above background. Substantial uptake did not begin until after the 11th day. Farrar (1953) and Walker (1958) did not observe such a long delay in uptake. The difference between the studies can be attributed to application techniques and weather conditions. Farrar (1953) applied the ^{32}P directly to the tree roots and Walker (1958) applied a solution containing labelled phosphoric acid. The CSP used in this study was applied in a granular form to the litter, and these granules persisted until after the rain on the 7th day. Uptake was probably rapid once the radioactive P reached the mineral soil. Riekerk and Gessel (1965) have shown that soluble phosphate leaches readily through the litter.

There is no published information on the initial uptake of ^{15}N by mature trees which compares with this work. Nommik and Popovic (1967) found ^{15}N in the foliage at their first sampling date which was 7 days after application. The ammonium sulphate pellets, applied in the study reported here, dissolved very soon after application. However, the ^{15}N was not detected

in the crown until the 7th day. Once the ^{15}N reached the xylem stream, the movement to the crowns was probably rapid. There are several possible explanations for the delay in reaching the xylem stream. Because of dry conditions the nitrogen probably did not diffuse down through the litter layer to the roots during this period. Pine mycorrhizae occurred in high numbers at the litter-mineral soil interface and in the top 10 cm of the mineral soil, but under the dry conditions which prevailed it is likely that the mycorrhizae were not active in nutrient uptake.

Hill-Cottingham and Bollard (1965) have suggested that all N entering the roots of apple trees pass through a transitory storage phase. This could provide another explanation to the delay in fertilizer-N uptake. Hill-Cottingham and Bollard (1965) also suggest that one of the effects of N fertilization is to stimulate mobilization of stored reserves. This could explain the rapid rise of N concentrations in the current needles prior to the detection of applied ^{15}N. Data in Figure 11 indicate that the rise of N concentration probably did not occur in the control trees. However, foliage samples were not collected between 0 and 6 weeks for these trees.

The initial uptake patterns for both isotopes show higher amounts accumulating in the lower crown foliage (Table 6 and Figures 8, 9). These data are expressed on a per gram basis and do not take into account the differences in foliage mass by ages or crown potition. The estimates of ^{15}N and ^{32}P

uptake into foliage of various parts of the crown are given in Table 24 and emphasize the uptake into the lower crown. This large movement of isotopes to the lower crown was directly related to the distribution of foliage, for both transpiration and the demand for nutrients are closely related to foliage mass.

This does not explain why there was a lower accumulation of tracers in the upper parts of the crown when the data were expressed on a per unit dry weight basis. The source of nutrients moving to various parts of the crown may provide a possible explanation. Nelson, Switzer, and Smith (1970) have shown movement of N and P out of the wood and bark during the early part of the growing season. If these woody tissue reserves were mobilized during the period that initial uptake was studied, then tracers moving from the roots would become more dilute as they traveled higher up the crown. Furthermore, the total N and P concentrations in the actively growing needles of the current flush did not show differences with crown position (Table 6). The total amount of N and P needed per gram of newly forming tissue is the same at all crown levels. Since the isotope levels were expressed on a per unit dry weight basis, the low amounts in the upper parts of the crown support the dilution hypothesis.

One implication of this hypothesis is that the upper crown foliage obtains a larger proportion of its N and P from internally stored material than the lower crown - when considered on a unit weight basis. The results of the

Table 24. Estimated ^{15}N and ^{32}P uptake into the foliage of a high-N treated tree, ten weeks after fertilization.

Foliage component	Estimated dry weight[a]	^{15}N absorbed	^{32}P absorbed
	g	μeq	cpm x 10^4
Terminal-1969	160	440	40
Terminal-1968	230	230	64
Upper crown-1969	1,160	4,010	432
Upper crown-1968	1,710	3,640	662
Lower crown-1969	1,740	8,440	778
Lower crown-1968	2,560	7,990	1,577
Total	7,560	24,749	3,553

[a]Dry weights are based on the assumption that the 1968 foliage had the same dry weight and distribution in the crown as the 1970 foliage at harvest. The 1969 foliage weights were calculated by use of a ratio of 1969 individual needle weights to that of the 1968 needle weight at 10 weeks after fertilization. The 1967 foliage was ignored as almost all of it had been shed.

depletion of the N from the soil indicate that the fertilizer-N was no longer of great importance to the nutrition of the tree during the 1970 growing season (see results, page 98). Hence, the main source of ^{15}N moving to the 1970 flush would have been from internally stored compounds. The tendency in this second growing season should be for the current foliage in the upper parts of the crown to have higher ^{15}N levels than the lower. This was the case; at harvesting the ^{15}N levels in the current foliage of the terminal leader were significantly higher than the current foliage of either the upper or lower crown branches.

One major difference between the two isotopes during the initial uptake period was the relative differences in accumulation by different foliage ages. It was found consistently that the ^{15}N accumulated at higher levels per unit dry weight in the current flush when compared to older foliage at the same crown position (Table 6). The ^{32}P accumulated at higher levels in older foliage. The same relationship was found when uptake data were expressed as the estimated quantities in foliage of different ages at 10 weeks after fertilizer application (Table 24).

The demand or 'sink' for N was higher in the rapidly expanding needles than in the older foliage. Greater quantities of tagged N accumulated in the younger foliage even though the younger foliage had lower dry weights than the older foliage. This uneven distribution of ^{15}N between various ages of foliage is in accord with the findings of

Nommik (1966). He suggested that the differing distribution was best explained by consideration of the basic metabolism in leaves of varying foliage ages. In young leaves the predominant process is synthesis of new protoplasm, which results in growth, and hence a high demand for N. In older needles photosynthesis is the dominant function and this leads ultimately to degenerative functions as senescence occurs.

The higher amount of ^{32}P in older foliage is more difficult to understand. Although Walker (1958) reported similar results for loblolly pine, other investigators found the highest ^{32}P activity in current foliage (Farrar, 1953; Tamm, 1955). Biddulph (1951), in studies with bean plants, found that the highest relative concentration of ^{32}P invariably occurs in the region of highest growth rate. Wright and Barton (1955) described a positive relationship between transpiration and ^{32}P accumulation in leaves. Hence for ^{32}P to accumulate in older needles at a time of current needle expansion suggests either a higher demand for P by the older needles, or that P is moving mainly by mass flow in the transpiration stream, and that the older needles are transpiring at a higher rate.

As transpiration rates of various foliage ages were not measured in this study and as information from other studies is variable, it is not wise to speculate on the importance of this mechanism in the transport of nutrients to foliage of different ages.

In the study of long-term foliar changes the P content of the older (1968) needles did not change with time (Table 8). Similarly the P content of the 1969 needles decreased very little in their second growing season. In the initial uptake study there was a slight drop in P concentration in the upper older foliage, but an increase in the lower older foliage. Overall the change in P concentration was not significant (Table 8). Apparently P was not moving out of the older foliage to any great extent. This in itself is unusual for P has been found to decline in older foliage during the growing season. A second unusual feature was the high P levels in older foliage, which were about 0.16 percent and were higher than the current foliage (Figures 8, 16). The Al levels in the older foliage were also very high, and the P to Al ratio remained relatively constant after the needles had finished their first season's growth (Figures 19, 20). Conceivably P in these older tissues is rendered physiologically inactive by the Al and that a metabolic demand for P existed in the older foliage. The mechanism could be similar to those suggested for P-Al interaction in roots (Clarkson, 1966). These were the precipitation of aluminum phosphates and the reduced phosphorylation of sugars.

At some crown positions, ^{32}P uptake into the younger foliage paralleled uptake into the older foliage, but was always lower (Figure 9). This indicates that after an initial demand for P by older foliage was met, P moved relatively uniformly to both young and old foliage.

The linear nature of P uptake from the 3rd to 10th week agrees well with other studies. In particular, Morrison (1962) demonstrated linear P uptake with time for young mycorrhizal pine. Walker's (1958) results differed slightly in showing a higher activity the 2nd day after ^{32}P application than at the 8th day. After the 8th day uptake was linear.

The linear nature of P uptake indicates that phosphate fertilizer availability and the uptake processes themselves did not change greatly over this period of time. The total amount of P taken into the foliage of the tree from the fertilizer was calculated using the estimates in Table 24 and the measured activity of the fertilizer sample. At the end of 10 weeks, only 0.7 percent of the fertilizer was accounted for in foliage.

The pattern of ^{15}N uptake with time was very different from that of ^{32}P (Figures 9, 10). The decrease in uptake after about 7 weeks was also apparent in the long-term foliar ^{15}N atom percent levels (Figures 21, 22). Whereas ^{15}N atom percent reached a maximum at 12 weeks, ^{15}N needle content in the current foliages reached a maximum in mid-winter. The estimate of ^{15}N absorbed by the foliage of a high-N tree at 10 weeks indicated some 10.5 percent of the fertilizer-N was in the foliage. Of this amount, 52 percent or about 12.9 meq excess ^{15}N was in the current foliage and 48 percent or 11.8 meq was in the older foliage.

The amount of ^{15}N in the 1968 and 1969 foliage of the high-N treated trees in January 1970 was estimated to be 8.5 and 14.6 meq excess ^{15}N. This estimate is based on the mean of all high-N treated trees. The estimate assumes that both 1968 and 1969 foliage have the same dry weight, and both are equal to the 1970 foliage dry weight (4,500 g/ tree) at harvesting. The uptake into the foliage in January 1970 was about 9.8 percent of the fertilizer applied. Thus, there was no substantial change in the total ^{15}N in the foliage between 10 and 36 weeks. At harvesting (December 1970), only 4.3 percent of the applied N was recovered from the foliage. However, the 1969 foliage had largely been shed from the trees by this time. Most of the uptake of labelled N into the foliage had taken place in the first three months after fertilizer application.

Transfer Within Trees

It was observed that during the summer of 1969 the previous season's issue of needles decreased in dry weight and N content. The change in ^{15}N content from the 6th week on was not significant (Table 8). The 1969 foliage also showed a decrease in dry weight, N, and ^{15}N content during the summer of 1970. Similar trends have been noted previously (see page 24 of literature review) and have been attributed primarily to redistribution. However, leaching could explain part of the observed reduction in dry weight and N content.

The loss of N from 1969 needles of the high-N treated trees was equivalent to 46 percent of the total N and 57 percent of the ^{15}N absorbed per needle (Figures 22, 23). These losses occurred between January and late August, 1970, before fall of the 1969 foliage. On a per needle basis, this loss was equal to 1.09 mg N and 0.44 μeq ^{15}N. During this same period the 1970 foliage accumulated 1.01 mg N and 0.25 μeq ^{15}N per needle. This may be expressed on a per tree basis by assuming that the 1969 foliage in January had about the same dry weight as the 1970 foliage at harvesting. The loss of N from the 1969 foliage on the high-N treated tree between January and October 1970 was approximately 21 g N and 8.2 meq ^{15}N. In the same time period the 1970 issue of needles accumulated 24 g N and 6.4 meq ^{15}N. This emphasizes the importance of internal transfer of nutrients from older to younger foliage.

The ^{15}N atom percent (or percent N from the fertilizer) decreased slightly with time, whereas ^{15}N content increased with time in the 1970 foliage (Figures 21, 22). Thus the amount of unlabelled N accumulating in the foliage increased in relation to the availability of ^{15}N. A probable explanation is that the amount of ^{15}N being redistributed in the tree declined during the growing season.

In late autumn and winter the dry weight and N content of older foliage increased. This occurred prior to needle abscission and has not been a general observation in other research (see page 24 of literature review), although Lowry and Avard (1969) observed a similar increase in older needles of Jack pine. It is probably related to maturation of the current needles with a resulting drop in the demand for organic compounds and N from older needles. Growth processes are influenced by climatic factors such as temperature and moisture availability.

Needle abscission is also related to climatic factors including rainfall. There were obvious differences in the time at which needle cast occurred during the period of the experiment. The 1967 issue of needles were late in falling and were not cast until July 1969. The 1968 needles were shed by March 1970. In northern Florida, the dry season is from September to December and rainfall for this period was 268, 535, and 149 mm for 1968, 1969, and 1970, respectively. The early loss of 1970 foliage is probably related to this low rainfall.

Labelled N Recovered from Ecosystem

After two growing seasons, 10.5 percent of the applied N was recovered in the trees; 8.9 percent occurred in the above ground portions of the tree and 1.6 percent in the roots. Nommik (1966) and Bjorkman, Lundeberg, and Nommik (1967) obtained about 7 percent recoveries of N in the above-ground portions of Scots pine fertilized with ammonium sulphate. However, Bjorkman, Lundeberg, and Nommik (1967) estimated that 9 to 12 percent of the applied N was in the roots - a figure substantially higher than recovered in the experiment described here. There are several differences, apart from species, which explain the discrepancy. Their experiment was over a shorter period (5 months) and tree roots had been cut with sheets of iron placed in the soil which may have influenced uptake. In addition the harvested roots included roots from the heavy ground vegetation. This vegetation absorbed 2 to 10 percent of the applied N into their above-ground parts.

Of the N recovered in the above-ground parts of the trees at harvesting, 48 percent was in the foliage, 36 percent in the tree stem and 16 percent was in the branches. Nommik (1966) found 64 percent of the N in the foliage after two growing seasons, 10 percent in the stem, and 26 percent in the branches. Bjorkman, Lundeberg, and Nommik (1967), after one growing season, found 74, 16, and 10 percent of the absorbed N in the foliage, wood, and branches, respectively.

The distribution of labelled N differed among the three experiments as a result of the early loss of 1969 foliage and the greater stem volume of the slash pine.

The amount of labelled N recovered in the total ecosystem was 49 percent of that applied (Table 18). The two treatments that included ^{15}N did not differ significantly. Bjorkman, Lundeberg, and Nommik (1967) recovered 79 percent of the N in their ammonium sulphate plots. In their experiment, which lasted a single growing season, the trees were isolated by buried iron sheets. They recovered 58 percent of the applied N from the soil. In contrast, the experiment described here with slash pine was a more 'open' system and lasted about 19 months. Some 23 percent of the applied N was recovered from the soil and litter.

Leaching of the N may have resulted in the low recovery of ^{15}N but the results are inconclusive. Tagged N was found below the surface 10 cm at all sampling dates following fertilizer application (Figures 25, 26). As expected, the amount of N moving down the profile (to 50 cm) was greater in the high-N treated plots (Appendix D). The largest changes in tagged N in the litter and A_1 horizon occurred in the first 12 weeks after fertilizer application (Figures 24, 27) and this indicated that if leaching had occurred it was mainly confined to this initial period. There was 245 mm rainfall reaching the forest floor during the initial 10 weeks, a factor which would argue for leaching of soluble N. The sampling at 6 weeks from the high-N

treated plots (after 84 mm rainfall) revealed substantial amounts of ^{15}N down to 40 cm depth (Appendix D). This ^{15}N declined rapidly in the following 6 weeks. The changes in labelled N were relatively minor after the 12th week.

The amounts of ^{15}N detected between 50 and 200 cm depth were negligible. Little N would have been expected to be held in the A_2 horizon where organic matter and CEC were low (Table 26). The N may have leached beyond the 200 cm sampling depth, although some indication of labelled N should have been found in B_2h horizon.

Low nitrate levels in these soils (Table 23), and other work with acid forest soils (see page 10 of literature review), suggested that little nitrification occurred. Hence, N leaching as nitrate probably did not occur. The lowering of the pH by the ammonium sulphate fertilizer was substantial in the upper 30 cm of the soil (Table 22). Lowering of pH could be explained by the removal of NH_4^+ from the system due to plant and microorganism uptake, or by nitrification, and denitrification. No measurements on denitritication were made.

The 'open' nature of the system may provide part of the answer to the low recovery of N. This implies that the N was dispersed more widely throughout the system than was anticipated in sampling. One possible place where losses could have easily occurred was through litter fall which escaped the sample plots. The 1968 and 1969 foliage shed from a single high-N sample tree, was estimated to have

contained 16 to 17 meq of ^{15}N excess. This was equivalent to about 7 percent of the applied fertilizer. With inclusion of surrounding trees, the loss was about 18 percent of the applied N. This would be a maximum figure for some of the litter would have fallen on the sample plot. Other possible means of dispersion would be through foliar leaching, uptake by other unsampled trees in the stand, and by lateral movement of the fertilizer. However, it does not appear that these types of dispersion can account fully for the low recovery of tagged N.

In other situations the recovery of applied N may be higher than the 49 percent obtained in this experiment. A higher uptake of N could be expected if the trees were deficient in N. Furthermore, on most woodland sites the ground vegetation is more prolific than on the old field site used in this experiment. A heavy ground vegetation would rapidly take up N and thus reduce losses by leaching or denitrification. In soils with a higher CEC there would be less possibility of NH_4^+ leaching.

Labelled N in the Trees

At harvest, levels of ^{15}N in the tree components suggested that the ^{15}N was associated with metabolically active substrates. Thus, the highest ^{15}N atom percent was in the foliage, buds, and in the branches formed since fertilization (Table 10). Within the stem the 1969-70 wood had higher levels of ^{15}N than either the old wood or bark. The bark samples included the cambium and phloem which should have been high in ^{15}N; the large amount of dead material in the outer bark lowered the ^{15}N level. The ^{15}N levels in the older pre-1969 wood demonstrated that the N was translocated into wood formed prior to fertilizer application.

The amounts of N incorporated into the old wood is surprisingly high, and is of the same order as that in the branches. The total amount of ^{15}N in the young wood and bark are both similar to that in the old wood. However, on a unit volume of wood basis the amount of fertilizer-N in the recent wood was very much higher than in old wood. Wood formed in 1969-70 accounted for 13 percent of the total stem volume. The wood samples were collected during the winter, a time that N has been reported to accumulate in the stem (Nelson, Switzer, and Smith, 1970). Thus, a substantial amount of this N would have been available for subsequent growth.

The branches formed during the two growing seasons of the experiment contained not only higher levels of ^{15}N, but

also larger amounts than the older branches (Table 10). This once again emphasizes the accumulation of N in actively growing regions. The dead branches also contained N derived from the fertilizer but the ^{15}N atom percent and the amount of ^{15}N incorporated were lower than in the live branches. The dead branches were from the base of the live crown and had been initiated prior to fertilization. Apparently labelled N had moved into these branches and had not been translocated completely before death.

The highest ^{15}N levels in the roots were in the laterals from within the fertilized plots. This indicates, as was expected, that the fertilizer was mainly absorbed through these laterals. The low ^{15}N levels in the roots from outside the fertilized area, were either due to translocation within the root or to lateral movement of the fertilizer. The taproots had lower ^{15}N levels than the inner laterals. It is not possible to conclude if this indicates uptake by taproots, or translocation within the root system, or both.

Response to N Treatment

The general lack of growth response indicates that N was not limiting growth on this site. The two levels of fertilizer applications caused substantial differences in the amount of absorbed ^{15}N, but these differences were not always reflected by either N concentrations, or total N content of the plant. The apparent discrepancy resulted from labelled ^{15}N forming a small proportion of the total N in the plant. Furthermore, the ^{15}N became dispersed within the tree with time. In the second winter, when the trees were harvested, the N derived from the fertilizer accounted for 4 and 12 percent of the total N in the trees of the low- and high-N treatments.

The amount of N supplied in the fertilizer did not make up a large proportion of the total N in the litter and A_1 horizon. At the start of the experiment the high-N treatment increased the total N in the soil by 10 percent. At the end of the experiment the fertilizer N remaining in the soil was only 1 percent of the total N.

The observed responses to N treatment were modified by plot size. The uptake and hence, response in N concentration in the needles, would have been greater if the plot size had been greater. The roots of the sample trees extended out 4.3 m from the edge of the fertilized area. Some 56 percent of the total fine absorbing roots occurred outside the plot.

Foliage Sampling

Foliar analysis is one of the main techniques used to diagnose nutrient deficiencies and to follow nutrient uptake. Several results from this study have important implications for the technique's use.

In the study of initial uptake of the fertilizers between May and July 1969, the main differences in N and P levels in the tree crowns were those associated with foliage age. Similarly, when the trees were sampled at harvesting in December 1970, the N concentration of the current foliage was the same in the terminal leader, upper crown, and lower crown. Hence it is not critical from which crown level or order of branch that current foliage is collected for analysis of these two elements. This result has not been generally reported by other investigators (see literature review, page 24). However, some of these workers made their conclusions without statistically testing their data. Smith, Switzer, and Nelson (1970) reached a similar conclusion with regard to so-called dormant season. In sampling foliage to follow the uptake of tracers it is important to take into account crown level. Significant differences with crown level were observed for both ^{32}P and ^{15}N during the study of initial uptake. The isotopes were higher in the lower crown. Moreover, the ^{15}N level was higher in the upper crown at the end of the second growing season.

Large seasonal fluctuations in P and N concentrations

must be taken into account in foliar sampling. Similar trends have been reported by other workers. The fluctuations are much less when the results are expressed on a weight per unit length of needle basis. However, to obtain data in this form requires more effort as it introduces two other variables, needle weight and needle length. This may make the method impractical for many studies.

The response of N foliar concentration to N fertilization was most marked during the summer of application. The difference among treatments had diminished greatly by winter and almost completely by the following summer (Figure 11). For following uptake of fertilizers it is therefore an advantage to sample at times other than the cool season. The selection of winter as the standard sampling period is usually on the basis of a stable foliage level. However, as Lowry and Avard (1969) have shown, this is not always the most sensitive period to detect differences in nutrition. Lowry and Avard (1969) reported on samples collected from a wide range of sites, whereas, this study extende their conclusion to differences between nutritional treatments on the same site. Smith, Switzer, and Nelson (1970) came to a similar conclusion.

Future Research

Some aspects of the research require further investigation.

The most important questions, for the widespread utilization of nitrogenous fertilizers are the possible losses by either leaching or denitrifation. Associated with leaching, is the necessity to investigate nutrient uptake by the deep taproots.

The internal storage and transfer of nutrients in trees is one of the two major nutrient cycles, but many aspects are poorly understood. The theory put forward by Hill-Cottingham and Bollard (1965) that fertilization mobilizes stored reserves, needs to be clarified. The factors which influence the storage and mobilization patterns of stored compounds need further study.

A relationship between P and Al was suggested by the initial uptake patterns of ^{32}P and by the high P and Al levels in older tissue. However, there is no proof that the relationship was more than a casual one and this needs to be established. If the relationship is a real one, Al must also be taken into account when setting critical levels for P deficiency in foliage.

SUMMARY AND CONCLUSIONS

The movement of N and P in an 11-year-old slash pine forest was followed using labelled fertilizers. Ammonium suphate, labelled with 2.388 atoms percent ^{15}N, was applied at three rates; 0, 56, and 224 kg N/ha. Concentrated superphosphate was applied as a basal dressing to all plots, at a rate of 96 kg P/ha, with two of the high-N plots receiving 15 millicuries ^{32}P each. Each plot consisted of a single codominant tree and the fertilizer was applied to an area of 1.5 m radius around each tree. There were four replications of the treatments.

The initial uptake of N and P were followed in the two trees that received the ^{32}P. The long-term changes in ^{15}N levels and N, P, and Al concentrations in the foliage were followed over two growing seasons. Soil and litter samples were collected at intervals to follow movement of the tagged N down the soil profile. At the end of the second growing season, the trees were harvested and all other parts of the ecosystem sampled so that the distribution of labelled N in the ecosystem could be quanitatively determined.

Dry weather and dry soil conditions delayed phosphate uptake by the trees for one week. The uptake of the tagged N was also delayed for a similar period of time. However,

the reason for this delay is not clear, as the ammonium sulphate dissolved soon after application. It may have resulted from the slow downward movement of N in the litter, or possibly from the inactivity of mycorrhizae due to the dry conditions. A third possibility was a temporary storage of the N in the roots before uptake in the foliage.

Higher amounts of ^{32}P and ^{15}N accumulated in the lower crown leaves during the first 10 weeks of the study. This is adequately explained by dilution from mobilized storage compounds within the tree crown. The ^{15}N accumulated in the current needles which grew rapidly and had a high metabolic demand. In contrast, the ^{32}P accumulated in the older needles. The reason for ^{32}P accumulation in these needles may be related to an Al-P interaction causing a physiological deficiency. As transpiration was not measured the influence of this factor could not be evaluated.

The ^{32}P showed a linear uptake into the foliage after the first three weeks. The accumulation of ^{15}N in the foliage was rapid between the 3rd and 6th week after fertilization. The current needles at fertilization reached their maximum ^{15}N content during the first winter.

In the 2nd growing season almost 50 percent of the total N in the previous season's flush of needles was lost by transfer to the current flush or by foliar leaching. The P from these older needles was not transfered to the current flush.

When the trees were harvested at the end of the second growing season 8.9 and 1.6 percent of the applied N was recovered from the above ground portions and roots, respectively. Of the labelled N in the above ground parts, 46, 36, and 16 percent were recovered from the foliage, stem, and branches, respectively. The uptake of N had a linear relationship with N fertilizer rate (0, 54 and 224 kg N/ha). The highest ^{15}N levels were associated with the needles, buds, lateral roots within the fertilized area, and in those parts of the branches and stemwood formed in the two previous growing seasons. There was evidence of transfer of ^{15}N to the roots outside the fertilized area and into wood and branches laid down prior to fertilizer application.

The recovery of labelled N in the ground vegetation at harvesting was negligible. However, the surrounding trees were estimated to have absorbed 15 percent of the applied N. The amount remaining in the soil was about 25 percent so that the total recovery in the ecosystem was about 50 percent of the N applied.

The low percentage recovery of applied N was difficult to explain. General dispersion through the ecosystem, as for example, by leaf fall, was able to account for part of the loss. Denitrification and leaching also may have been important during the initial three months, for the amount of N in the soil declined rapidly during this time. It was apparent that movement through the litter had been rapid and that some leaching in the mineral soil had occurred.

The P and N concentrations in current needles were not influenced by crown level or branch order from which the samples were collected. However, they did show distinct age differences and seasonal patterns. Needle fall was thought to be related to the severity of the drought between September and December.

Foliage N concentration showed an increase to the high rate of N fertilizer. However, this increase had largely disappeared by the spring of the second growing season. The cause was apparently due to redistribution of the N within the tree.

The following conclusions can be drawn from these results:

1. Applied N and P initially accumulate in greater quantities in lower crown foliage than in other foliage of 11-year-old slash pine, apparently as a result of mass transport.
2. Upper crown foliage receives less fertilizer-N and -P than the lower crown foliage (on a per unit dry weight basis), as a result of dilution by translocation of compounds stored in the tree crown.
3. Nitrogen from the soil accumulates in higher amounts in expanding needles than in mature needles, as a result of rapid protoplasm synthesis. Phosphorus accumulated in higher quantities in older foliage than in current foliage. This may have been related to an Al-P interaction in the older needles.

4. Phosphorus uptake is initially linear with time after the fertilizer reaches the rooting zone of this flatwood soil. In contrast, the uptake of N is non-linear as the availability form the soil declines rapidly with time.

5. Nitrogen from 1-year-old needles is translocated to newly developing tissues during the growing season. There is an increase in N content and dry weight of the needles in the second winter following needle initiation.

6. At the end of two growing seasons, labelled N still accumulates in regions of high metabolic activity such as the foliage, buds, and recently formed wood and branches.

7. In sampling for N and P foliar analysis it is not necessary to collect needles from any particular crown position. However, the age of the foliage and season of sampling are important factors. For N, sampling during the growing season had an advantage over sampling in the winter.

8. Approximately 50 percent of the applied N was accounted for in the forest ecosystem. This recovery seems quite low, but it is in line with values obtained for many agricultural crops. It may be partially explained by a low recovery in litter from treated trees and dispersal in the ecosystem.

APPENDIX A

Soil Description

Table 25. Profile descriptions of soil at experimental area.

Depth cm	Horizon	Description
		Tavares sand - plot 7
4-0	A_0	Litter layer of pine needles.
0-23	A_{11}	Grey (10 YR 5/1) sand; very friable crumb; common uncoated light grey single sand grains; gradual boundary.
23-51	A_{12}	Very dark grey brown (10 YR 3/2) sand; single grain; loose; gradual boundary.
51-88	A_{21}	White (10 YR 8/2) sand; common large mottles of light yellowish brown (10 YR 6/4) with smaller reddish yellow mottles (7.5 YR 6/8); single grain structure; friable; gradual boundary.
88-120	A_{22}	Very pale brown (10 YR 7/3) sand; common light yellowish brown (10 YR 6/4) and reddish yellow (7.5 YR 6/9) mottles; friable; single grain structure; distinct boundary.
120-148	A_{23}	Pinkish grey (5 YR 6/2) with a few very dark red (2.5 YR 2/2) and reddish yellow (7.5 YR 6/8) mottles; single grain structure, friable; distinct boundary.
148+	B_2h	Black (5 YR 2/1) and dark reddish grey (5 YR 4/2) sand; massive hard consistence.
		Tavares sand - plot 9
2-0	A_0	Litter layer of pine needles.
0-19	A_{11}	Grey (N 5/) sand; loose; common uncoated light grey sand grains; gradual boundary.

Depth	Horizon	Description
		Tavares sand - plot 9
19-49	A_{12}	Dark brown (10 YR 3/2) sand; single grain; loose; gradual boundary.
49-99	A_{21}	Light grey (10 YR 7/2) sand with occasional reddish yellow (7.5 YR 6/8) mottles; weakly coherent; gradual boundary.
99-126	A_{22}	Very pale brown (10 YR 8/4) sand with yellow (10 YR 7/6) mottles; weakly coherent; gradual boundary.
126-188	A_{23}	White (10 YR 8/2) sand with very small occasional yellow mottles (10 YR 8/6); loose single grain structure; distinct boundary.
188+	B_2h	Brown (10 YR 4/3) sand; single grained, very friable structure.

[a] Color by Munsell chart; texture by particle-size analysis.

Table 26. Selected characteristics of the Tavares sand at the experimental site, Austin Cary Forest.

Soil depth	Particle size distribution[a]							OM	Bulk density	CEC
	VCS	CS	S	FS	VFS	Silt	Clay			
	%								g/cm^3	meq/100g
0- 10	0.1	8.1	48.4	31.9	3.3	5.5	2.7	1.72	1.32	3.52
10- 20	0.0	5.5	48.4	33.3	4.7	5.1	3.1	1.36	1.47	2.82
20- 30	0.1	5.5	46.2	36.7	4.1	3.9	3.4	1.28	1.52	2.49
30- 40	0.1	6.5	45.6	36.8	4.0	4.1	3.0	1.05	1.53	2.19
40- 50	0.1	8.0	41.0	37.4	6.1	3.7	3.7	0.68	1.58	1.69
50- 60								0.25		0.38
60- 80	0.0	6.7	40.1	40.1	8.1	3.9	1.1	0.26	1.61	0.52
80-100	1.4	12.4	45.2	35.7	0.4	3.8	1.1	0.26	1.71	0.52
100-120	1.5	12.1	44.6	33.9	3.9	2.9	1.1	0.23	1.74	0.34
120-140	0.2	11.0	37.7	31.7	4.3	9.1	6.0	0.15	1.89	0.64
140-160	0.2	12.8	48.7	28.7	2.1	5.1	2.9	0.66	1.66	1.20
160-180	0.5	3.3	46.5	36.9	4.6	6.2	2.0	0.70	1.68	1.45
180-200	0.1	10.1	44.3	33.2	3.7	5.7	2.9	0.57	1.65	2.23

[a]VCS Very coarse sand.
CS Coarse sand.
S Sand.
FS Fine sand.
VFS Very fine sand.

APPENDIX B

Initial Uptake of N and P into Trees

Data

Statistical Analysis of Initial Uptake Data

Table 27. Initial uptake of N and P for the first 10 weeks after fertilization. Values are averages for two trees.

Days after application	Location in crown	[a]	P	N	^{32}P	^{15}N	^{15}N absorbed/g	Fertilizer N
			%		net cp^m/g	atom %	µeq	% of total
1	T	69	-	0.85	-	0.368	0.00	0.00
1	T	68	-	0.82	-	0.368	0.00	0.00
1	U1	69	-	0.86	-	0.368	0.00	0.02
1	U1	68	-	0.79	-	0.368	0.00	0.02
1	U2	69	-	0.78	-	0.367	0.00	0.00
1	L1	69	-	0.90	-	0.368	0.00	0.02
1	L1	68	-	0.83	-	0.367	0.00	0.00
1	L1	67	-	0.69	-	0.367	0.00	0.00
1	L2	69	-	0.86	-	0.366	0.00	0.00
1	L2	68	-	0.82	-	0.367	0.00	0.00
1	L2	67	-	0.67	-	0.366	0.00	0.02
3	T	69	0.151	0.97	4	0.367	0.00	0.00
3	U1	69	0.146	0.93	6	0.368	0.00	0.00
3	U2	69	0.141	0.85	4	0.367	0.00	0.00
3	L1	69	0.133	0.86	0	0.366	0.00	0.00
3	L2	69	0.127	0.82	0	0.367	0.00	0.00
5	T	69	0.144	1.04	0	0.368	0.00	0.02
5	T	68	0.150	0.77	7	0.366	0.00	0.00
5	U1	69	0.138	0.97	7	0.367	0.00	0.00
5	U1	68	0.157	0.76	21	0.365	0.00	0.00
5	U2	69	0.140	0.94	0	0.367	0.00	0.00
5	L1	69	0.127	0.87	0	0.368	0.00	0.00
5	L1	68	0.156	0.85	10	0.368	0.01	0.04
5	L1	67	0.165	0.70	21	0.369	0.01	0.07
5	L2	69	0.134	0.88	28	0.369	0.01	0.07
5	L2	68	0.153	0.82	16	0.368	0.00	0.02
5	L2	67	0.167	0.72	8	0.368	0.00	0.02
7	T	69	0.156	1.08	10	0.367	0.00	0.02
7	U1	69	0.161	1.05	19	0.370	0.01	0.07
7	U2	69	0.158	0.97	10	0.370	0.01	0.10
7	L1	69	0.141	0.95	28	0.371	0.02	0.15
7	L2	69	0.145	0.88	31	0.372	0.03	0.22

Table 27. continued

Days after application	Location in crown		P	N	^{32}P	^{15}N	^{15}N absorbed/g	Fertilizer N
			%		net cp^m/g	atom %	µeq	% of total
11	T	69	0.157	1.07	48	0.377	0.07	0.45
11	T	68	0.160	0.89	78	0.376	0.05	0.40
11	U1	69	0.160	1.09	62	0.382	0.11	0.69
11	U1	68	0.167	0.86	77	0.379	0.07	0.54
11	U2	69	0.160	0.98	69	0.381	0.09	0.62
11	L1	69	0.142	1.00	66	0.393	0.17	1.21
11	L1	68	0.152	0.93	98	0.382	0.09	0.67
11	L1	67	0.169	0.74	128	0.383	0.08	0.72
11	L2	69	0.135	1.03	69	0.397	0.21	1.41
11	L2	68	0.157	0.92	109	0.383	0.10	0.74
11	L2	67	0.169	0.73	126	0.383	0.08	0.74
15	T	69	0.153	1.07	89	0.403	0.27	1.73
15	U1	69	0.151	1.03	128	0.426	0.43	2.87
15	U2	69	0.143	0.97	140	0.417	0.34	2.42
15	L1	69	0.141	0.99	151	0.449	0.57	4.01
15	L1	69	0.149	0.97	211	0.492	0.85	6.11
21	T	69	0.154	1.09	195	0.435	0.52	3.29
21	T	68	0.152	0.85	353	0.429	0.36	2.99
21	U1	69	0.149	1.04	302	0.458	0.66	4.43
21	U1	68	0.161	0.84	457	0.443	0.44	3.68
21	U2	69	0.149	0.97	308	0.462	0.65	4.65
21	L1	69	0.135	1.06	386	0.519	1.13	7.44
21	L1	68	0.164	0.94	608	0.462	0.62	4.65
21	L1	67	0.173	0.73	534	0.466	0.50	4.85
21	L2	69	0.147	1.04	576	0.576	1.54	10.26
21	L2	68	0.161	0.92	648	0.466	0.64	4.82
21	L2	67	0.169	0.73	635	0.476	0.56	5.32
28	T	69	0.155	1.05	545	0.503	1.01	6.68
28	U1	69	0.145	1.01	811	0.575	1.49	10.24
28	U2	69	0.144	0.98	847	0.566	1.37	9.77
28	L1	69	0.144	1.10	1182	0.680	2.44	15.43
28	L2	69	0.147	1.13	1380	0.730	2.92	17.88

Table 27. continued

Days after application	Location in crown		P	N	^{32}P	^{15}N	^{15}N absorbed/g	Fertilizer N
			%		net cp^m/g	atom %	µeq	% of total
35	T	69	0.147	1.03	662	0.602	1.73	11.57
35	T	68	0.155	0.86	1091	0.543	1.06	8.63
35	U1	69	0.137	1.03	1079	0.666	2.19	14.71
35	U1	68	0.169	0.90	1584	0.606	1.51	11.75
35	U2	69	0.146	0.97	1083	0.678	2.14	15.33
35	L1	69	0.135	1.09	1651	0.810	3.43	21.83
35	L1	68	0.173	1.06	2186	0.631	1.99	13.01
35	L1	67	0.182	0.81	1994	0.645	1.60	13.67
35	L2	69	0.140	1.13	2126	0.860	3.97	24.33
35	L2	68	0.172	1.06	2355	0.663	2.22	14.56
35	L2	67	0.187	0.83	2536	0.690	1.90	15.90
42	T	69	0.140	1.12	1154	0.660	2.35	14.44
42	U1	69	0.129	1.04	1771	0.795	3.16	21.11
42	U2	69	0.133	0.97	1658	0.757	2.69	19.21
42	L1	69	0.135	1.07	2010	0.839	3.61	23.29
42	L1	69	0.132	1.15	2930	0.927	4.60	27.62
49	T	69	0.137	1.01	1258	0.678	2.24	15.33
49	T	68	0.150	0.86	1586	0.591	1.35	11.03
49	U1	69	0.124	0.97	1635	0.775	2.82	20.10
49	U1	68	0.163	0.92	2204	0.667	1.96	14.79
49	U2	69	0.129	0.95	2033	0.800	2.92	21.36
49	L1	69	0.131	1.09	2782	0.910	4.22	26.81
49	L1	68	0.179	1.05	3523	0.745	2.81	18.62
49	L1	67	0.182	0.83	2984	0.731	2.15	17.93
49	L2	69	0.136	1.10	3382	0.997	4.94	31.11
49	L2	68	0.176	1.05	3441	0.741	2.78	18.42
49	L2	67	0.181	0.85	3149	0.763	2.40	19.51
56	T	69	0.135	1.04	1900	0.732	2.69	18.00
56	U1	69	0.125	1.00	2409	0.818	3.21	22.26
56	U2	69	0.126	0.91	2569	0.845	3.10	23.59
56	L1	69	0.123	1.05	3238	0.904	4.00	26.48
56	L2	69	0.128	1.08	4043	0.994	4.83	30.93

Table 27. continued

Days after application	Location in crown		P	N	^{32}P	^{15}N	^{15}N absorbed/g	Fertilizer N
			%		net cp^m/g	atom %	µeq	% of total
71	T	69	0.130	1.01	2494	0.744	2.72	18.60
71	T	68	0.146	0.83	2797	0.623	1.50	12.59
71	U1	69	0.119	0.96	3553	0.865	3.40	24.55
71	U1	68	0.152	0.89	3871	0.703	2.13	16.57
71	U2	69	0.120	0.97	3887	0.878	3.52	21.20
71	L1	69	0.123	1.03	5061	0.997	4.64	31.11
71	L1	68	0.170	0.98	5742	0.779	2.89	20.33
71	L1	67	0.184	0.85	5871	0.776	2.44	20.18
71	L2	69	0.114	1.07	3886	1.034	5.06	32.91
71	L2	68	0.169	1.10	6577	0.795	3.34	21.09
71	L2	67	0.177	0.89	6599	0.831	1.62	22.89

[a]T 69 = Terminal - 1969 foliage
T 68 = Terminal - 1968 foliage
U1 69 = Upper 1st-order branches-1969 foliage
U1 68 = Upper 1st-order branches-1968 foliage
U2 69 = Upper 2nd-order branches-1969 foliage
L1 69 = Lower 1st-order branches-1969 foliage
L1 68 = Lower 1st-order branches-1968 foliage
L1 67 = Lower 1st-order branches-1967 foliage
L2 69 = Lower 2nd-order branches-1969 foliage
L2 68 = Lower 2nd-order branches-1968 foliage
L2 67 = Lower 2nd-order branches-1967 foliage

Statistical Analysis of Initial Uptake Data

Samples were collected from two trees at 1, 3, 5, 7, 11, 15, 21, 28, 35, 42, 49, 56, and 71 days after treatment. On alternate days, beginning with day one, all ages of foliage were collected, but on the other days only recent (1969) foliage was collected.

The first day's data were not included for the P statistical analyses, but were included in the N analyses.

Two analyses of variance were run for each parameter. The first used only 1969 needles and included all days. This analysis was a three factor factorial, with both position-in-crown and days as fixed effects and trees as a random effect. The basic model was $X_{IJK} = \mu + A_i + B_j + C_k + AB_{ij} + AC_{ik} + BC_{jk} + ABC_{ijk} + \varepsilon_{ijk}$

where

μ = mean

A = location

B = days

C = trees

The appropriate F tests with this model were:

Test A with AC

Test B with BC

Test C, AB, AC, BC with ABC

The ABC interaction was assumed negligible and a measure of error for tests C, AC, and BC. This assumption was not needed for tests of A, B, or AB.

The second set of analyses used data from those dates where all ages of foliage were sampled. The location factor included both position-in-crown and foliage age. The model was essentially the same, except that there was one missing value which was estimated by covariance analysis.

In both analyses the position of location factor was subdivided into meaningful single degree of freedom contrasts.

In the following tables significance is denoted by:

* significant at 5 percent level of probability.

** significant at 1 percent level of probability.

*** significant at 0.1 percent level of probability.

The AC and BC interactions, although sometimes significant, were primarily calculated for testing the main effects.

Table 28. Analysis of variance of initial uptake of P into 1969 (current) foliage.

		% P		^{32}P cpm/g	
Source	df	ms x 10^{-8}	F	ms	F
Location (A)	4	55,849	2.48	2,744,593	7.85*
Day (B)	11	94,271	4.71**	16,581,960	159.26***
Tree (C)	1	1,008,333	201.65***	666,532	10.20**
A x B	44	5,467	1.09	324,134	4.96***
A x C	4	22,506	4.50**	349,452	5.35**
B x C	11	19,848	3.97***	104,116	1.59
A x B x C	44	5,000		65,316	

Table 29. Subdivision of location sum of squares into meaningful single degree of freedom contrasts - initial uptake of P into 1969 foliage.

	% P		^{32}P cpm/g	
	ms x 10^{-8}	F	ms	F
Terminal vs other locations	150,167	6.67	5,696,478	16.30*
Upper br vs lower branches	68,801	3.06	4,863,804	13.92*
Upper 1st-order vs upper 2nd-order	208	0.01	56,882	0.16
Lower 1st-order vs lower 2nd-order	4,219	0.19	361,209	1.03

Table 30. Analysis of variance of initial uptake of P into all ages of foliage.

		% P		^{32}P cpm/g	
Source	df	ms x 10^{-8}	F	ms	F
Location (A)	10	417,000	4.23*	4,299,740	10.27***
Days (B)	5	64,609	1.57	10,791,420	216.06***
Trees (C)	1	1,124,834	507.51***	2,310,796	36.18***
A x B	50	22,011	9.93***	1,018,340	15.94***
A x C	10	98,717	44.54***	418,731	6.56***
B x C	5	41,278	18.62***	413,315	6.47***
A x B x C	117	2,216		63,868	

Table 31. Subdivision of location sum of square into meaningful degree of freedom contrasts - initial uptake of P into foliage of all ages.

	% P		^{32}P cpm/g	
Contrast	ms x 10^{-8}	F	ms	F
Terminal vs other locations	66,144	0.67	19,077,898	45.56***
Upper br vs lower branches	433	0.00	11,370,094	27.15***
Upper 1st-order vs upper 2nd-order	6,344	0.06	246,669	0.59
Lower 1st-order vs lower 2nd-order	1,824	0.02	766,479	1.83
Age 69 vs 67, 68	2,648,522	26.83***	3,724,484	8.89*
Age 67 vs 68	414,481	4.20	25,954	0.06

Table 32. Analysis of variance of initial uptake of N into 1969 (current) foliage.

		% N		^{15}N atom %	
Source	df	ms x 10^{-8}	F	ms x 10^{-8}	F
Location (A)	4	3,127,039	4.33	8,147,003	29.96**
Day (B)	12	4,380,192	9.28***	46,614,856	644.07***
Tree (C)	1	468,000	1.25	116,401	1.53
A x B	48	515,913	1.38	528,756	6.94***
A x C	4	722,808	1.93	271,903	3.57*
B x C	12	471,833	1.26	72,376	0.95
A x B x C	48	375,183		76,182	

		µeq ^{15}N absorbed/g		% fertilizer N	
Source	df	ms x 10^{-6}	F	ms x 10^{-4}	F
Location (A)	4	5,999,293	35.59**	1,992,168	29.72**
Day (B)	12	25,378,124	256.67***	11,374,163	648.88***
Tree (C)	1	4,119	0.07	30,557	1.64
A x B	48	410,659	6.17***	129,352	6.96***
A x C	4	151,523	2.28	67,039	3.61*
B x C	12	98,875	1.48	17,529	0.94
A x B x C	48	66,562		18,573	

Table 33. Subdivision of location sum of squares into meaningful single degree of freedom contrasts - initial uptake of N into 1969 foliage.

	% N		^{15}N atom %	
Contrast	ms x 10^{-8}	F	ms x 10^{-8}	F
Terminal vs other locations	4,284,308	5.93	15,729,603	57.85**
Upper br vs lower branches	3,769,615	5.22	14,881,112	54.73**
Upper 1st-order vs upper 2nd-order	4,384,808	6.07	3,894	0.01
Lower 1st-order vs lower 2nd-order	69,423	0.10	1,973,402	7.26

	µeq ^{15}N absorbed/g		% fertilizer N	
Contrast	ms x 10^{-6}	F	ms x 10^{-4}	F
Terminal vs other locations	8,459,376	55.83**	3,840,494	54.29**
Upper br vs lower branches	13,786,047	90.98***	3,643,467	54.35**
Upper 1st-order vs upper 2nd-order	33,103	0.22	1,084	0.02
Lower 1st-order vs lower 2nd-order	1,718,701	11.34*	483,627	7.21

Table 34. Analysis of variance[a] of initial uptake of N into all ages of foliage.

		% N		^{15}N atom %	
Source	df	ms x 10^{-8}	F	ms x 10^{-8}	F
Locations (A)	10	12,111,243	23.41***	3,859,240	16.71***
Days (B)	6	9,609,571	66.51***	82,972,038	174.47***
Trees (C)	1	3,614,884	13.51***	3,597,897	67.61***
A x B	60	474,123	1.77*	596,826	11.22***
A x C	10	517,431	1.93	230,922	4.34***
B x C	6	144,473	0.54	475,575	8.94***
A x B x C	59	267,624		53,215	

		µeq ^{15}N absorbed/g		% fertilizer N	
Source	df	ms x 10^{-5}	F	ms x 10^{-4}	F
Locations (A)	10	303,845	29.87***	943,117	16.52***
Days (B)	6	4,074,920	299.14***	20,229,806	176.57***
Trees (C)	1	110,319	30.01***	891,938	69.16***
A x B	60	47,184	12.84***	146,094	11.33***
A x C	10	10,173	2.77**	57,104	4.43***
B x C	6	17,783	4.84***	114,572	8.88***
A x B x C	59	3,676		12,898	

[a] One df in the analysis was associated with estimating the missing value - it is not included in the tables.

Table 35. Subdivision of location sum of squares into meaningful single degree of freedom contrasts - initial uptake of N into foliage of all ages.

	% N		^{15}N atom %	
Contrast	ms x 10^{-8}	F	ms x 10^{-8}	F
Terminal vs others	1,956,093	3.78	13,033,634	56.44***
Upper br vs lower branches	12,863,623	24.86***	8,632,727	37.38***
Upper 1st-order vs upper 2nd-order	1,007,480	1.95	18,429	0.08
Lower 1st-order vs lower 2nd-order	212,600	0.41	829,878	3.59
Age 69 vs 67, 68	82,311,074	159.07***	18,864,896	81.69***
Age 67 vs 68	38,548,587	74.50***	91,247	0.40

	µeq ^{15}N absorbed/g		% fertilizer N	
Contrast	ms x 10^{-6}	F	ms x 10^{-4}	F
Terminal vs others	8,875,115	87.24***	3,192,776	55.91***
Upper br vs lower branches	8,664,639	85.17***	2,102,786	36.82***
Upper 1st-order vs upper 2nd-order	55,152	0.54	4,301	0.08
Lower 1st-order vs lower 2nd-order	695,050	6.83**	203,923	3.57
Age 69 vs 67, 68	17,672,162	173.71***	4,596,292	80.49***
Age 67 vs 68	1,446,311	14.22***	22,222	0.39

APPENDIX C

Long-Term Changes in Foliage Characteristics

Data

Statistical Analyses of Long-Term Foliage Collections

Data

Table 36. Long-term changes in dry weight, length, N, P, and Al concentrations and N levels in foliage of various ages.

Weeks after application	Treatment[a]	Needle weight	Needle length	N	P	Al	^{15}N excess	N from fertilizer	^{15}N absorbed
		mg	cm	—%—		ppm	atom %	%	µeq/g
				1968 Foliage					
0	1	199	24.8	0.86	0.12	503			
	2	240	25.4	0.83	0.11	684			
	3	218	24.8	0.82	0.14	600			
6	1	177	23.4	0.74	0.13	544			
	2	205	23.0	0.74	0.12	706	0.063	3.14	0.33
	3	192	23.2	0.90	0.16	660	0.229	11.36	1.47
12	1	184	23.0	0.71	0.14	550			
	2	190	22.2	0.67	0.12	712	0.073	3.62	0.35
	3	179	22.5	0.93	0.16	650	0.342	10.97	2.27
18	1	174	23.4	0.66	0.14	525			
	2	205	22.6	0.70	0.12	762	0.057	2.83	0.29
	3	172	22.3	0.86	0.14	675	0.333	16.52	2.04
24	1	165	22.6	0.70	0.14	550			
	2	199	23.4	0.64	0.13	714	0.070	3.47	0.32
	3	191	23.0	0.81	0.15	688	0.279	13.83	1.61
36	1	174	22.9	0.78	0.15	572			
	2	213	23.5	0.70	0.13	748	0.053	3.24	0.33
	3	201	23.5	0.78	0.15	697	0.293	14.45	1.64
42	1	183	23.4	0.77	0.14	562			
	2	240	23.2	0.70	0.12	738	0.050	2.48	0.25
	3	197	23.5	0.86	0.14	700	0.309	15.33	1.89
48	1	202	23.3	0.80	0.13	550			
	2	238	23.7	0.75	0.13	753	0.071	3.54	0.38
	3	214	23.4	0.83	0.13	694	0.294	14.45	1.73

Table 36. continued

Weeks after application	Treatments[a]	Needle weight	Needle length	N	P	Al	^{15}N excess	N from fertilizer	^{15}N absorbed
		mg	cm	%		ppm	atom %	%	µeq/g
				1969 Foliage					
0	1	26	5.6	0.86	0.12	181			
	2	36	6.3	0.94	0.12	217			
	3	39	6.5	0.87	0.34	184			
6	1	73	13.0	0.84	0.21	264			
	2	91	13.2	0.80	0.14	325	0.169	8.37	0.96
	3	96	14.6	0.97	0.12	306	0.443	21.97	3.08
12	1	108	18.1	0.82	0.11	294			
	2	124	18.6	0.80	0.11	362	0.170	8.44	0.96
	3	141	20.9	0.97	0.11	312	0.554	27.49	3.84
18	1	148	22.7	0.80	0.11	312			
	2	157	21.4	0.75	0.10	425	0.152	7.54	0.81
	3	182	24.2	0.96	0.09	376	0.530	26.30	3.62
24	1	148	22.8	0.80	0.11	337			
	2	181	22.7	0.80	0.10	436	0.142	7.06	0.82
	3	191	24.7	0.93	0.10	402	0.438	21.74	2.89
30	1	166	23.1	0.92	0.12	416			
	2	186	22.3	0.89	0.11	430	0.128	6.38	0.81
	3	204	24.8	1.02	0.11	433	0.458	22.75	3.33
36	1	169	22.8	0.95	0.12	400			
	2	202	22.4	0.92	0.11	512	0.119	5.90	0.78
	3	239	25.5	0.99	0.10	450	0.458	22.72	3.24
42	1	177	22.8	0.94	0.11	389			
	2	200	22.8	0.89	0.10	500	0.119	5.92	0.76
	3	216	24.6	1.03	0.12	464	0.446	22.12	3.28
48	1	165	22.0	0.94	0.12	407			
	2	211	22.3	0.87	0.10	550	0.124	6.15	0.70
	3	230	24.4	0.94	0.11	475	0.451	22.38	3.01

Table 36. continued

Weeks after application	Treatment[a]	Needle weight	Needle length	N	P	Al	^{15}N excess	N from fertilizer	^{15}N absorbed
		mg	cm	%		ppm	atom %	%	µeq/g
54	1	164	22.3	0.84	0.12	421			
	2	223	23.0	0.78	0.11	538	0.113	5.61	0.63
	3	206	24.2	0.82	0.12	450	0.415	20.59	2.44
60	1	168	22.7	0.74	0.12	435			
	2	213	23.3	0.70	0.10	570	0.111	5.52	0.56
	3	205	24.0	0.77	0.13	534	0.401	19.91	2.22
66	1	185	22.7	0.68	0.12	400			
	2	183	22.8	0.70	0.10	550	0.106	5.26	0.53
	3	184	23.0	0.70	0.13	500	0.366	18.16	1.82
72	1	166	23.6	0.62	0.12	450			
	2	155	24.0	0.61	0.11	600	0.104	5.16	0.45
	3	171	24.5	0.66	0.14	525	0.398	19.79	1.88
78	1	192	23.7	0.68	0.13	472			
	2	234	23.5	0.64	0.11	622	0.094	4.64	0.43
	3	225	25.0	0.66	0.14	569	0.348	17.28	1.64
				1970 Foliage					
54	1	52	9.4	0.90	0.12	200			
	2	69	10.0	0.85	0.12	225	0.093	4.62	0.56
	3	60	10.2	0.86	0.13	200	0.357	17.71	2.19
60	1	86	14.7	0.77	0.10	209			
	2	107	14.7	0.72	0.10	266	0.084	4.19	0.44
	3	100	15.1	0.78	0.11	247	0.409	17.55	1.98
66	1	124	19.6	0.76	0.10	250			
	2	145	19.7	0.72	0.09	325	0.082	4.07	0.42
	3	138	20.0	0.74	0.11	350	0.345	17.12	1.81

Table 36. continued

Weeks after application	Treatment[a]	Neddle weight	Needle length	N	P	Al	^{15}N excess	N from fertilizer	^{15}N absorbed
		mg	cm	%		ppm	atom %	%	µeq/g
72	1	192	23.4	0.78	0.10	280			
	2	248	21.6	0.76	1.10	350	0.080	3.97	0.43
	3	227	21.8	0.75	0.11	325	0.324	16.07	1.74
78	1	167	22.9	0.90	0.12	325			
	2	216	23.0	0.89	0.10	419	0.077	3.83	0.49
	3	185	22.9	0.88	0.15	378	0.310	15.37	1.96
84	1	168	23.4	0.96	0.11	353			
	2	194	22.0	0.87	0.10	437	0.675	3.35	0.42
	3	177	22.2	0.91	0.11	381	0.306	15.21	1.99

[a] 1. Control
2. 56 kg N/ha.
3. 224 kg N/ha.

Statistical Analysis of Long-Term Foliage Collections

The data consisted of 14 responses all concerned with foliage samples collected at 6 weekly intervals from a N fertilizer experiment with three rates (0, 56, and 224 kg N/ha) and four replications. A total of 11 samplings were made but in 7 of these the samples were bulked by treatment. Three different foliage ages were involved. The 1968 foliage was present for the first 8 samplings, the 1969 was available for all but the last sampling period and the 1970 flush was present after the 54th week.

The basic fertilizer experiment was a completely randomized design. The analysis followed a split-plot in time with fertilizer treatments and sampling dates as fixed effects. Because of the imbalance in foliage ages, each foliage age was treated separately.

Each analysis was made through a two-stage procedure. In the first part, all data for a particular response were involved with the mean being used if all replications had been sampled. This was analysed by the method of unweighted means. In the analysis, the variance was partitioned into treatment (A), time (B), and A x B components. The mean squares were adjusted by the harmonic mean of the original number of observations at each sampling date.

The second part of the analysis used only dates from which replications were available. This part of the analysis

was used to obtain the error terms for testing A, B, and AB from the first part of the analysis.

There were a few missing values and these were estimated. The degrees of freedom for error were adjusted to allow for this. Where ^{15}N data has been analysed, the control treatment and first sampling data have been ommited.

In the following tables the tests of significance have been denoted as follows:

* Significant at 5 percent probability level.

** Significant at 1 percent probability level.

*** Significant at 0.1 percent probability level.

Table 37. Analysis of variance of the seasonal trends in needle weight and weight/cm needle of the 1968 flush, as influenced by N treatment.

Source	df	needle weight		weight/cm needle	
		ms	F	ms x 10^{-4}	F
N Treatment (A)	2	4,425	1.28	84,959	3.11
Linear	1	381	0.11	2,525	0.09
Quadratic	1	8,726	2.53	167,393	6.13*
Error (a)	9	3,448		27,325	
Time (B)	7	1,218	2.44*	10,316	2.10
A x B	14	153	0.31	2,047	0.42
Error (b)	34	499		4,902	

Table 38. Analysis of variance of N concentration (% N), N content per needle, and N content per cm needle in the 1968 flush, as influenced by sampling date and N treatment.

		% N		N/needle		N/cm needle	
Source	df	ms x 10^{-6}	F	ms x 10^{-5}	F	ms x 10^{-7}	F
Treatment (A)	2	67,785	12.90**	30,080	1.05	5,779	2.79
Linear	1	104,419	19.88**	48,095	1.68	9,279	4.49
Quadratic	1	3,115	5.93	12,064	0.42	2,279	1.10
Error (a)	9	5,251		28,546		2,068	
Time (B)	7	7,387	3.88**	17,340	4.33*	1,753	3.84**
A x B	14	5,309	2.79**	1,897	0.40	336	0.74
Error (b)	34	1,902		4,006		456	

Table 39. Analysis of variance of N concentration (% N), N content per needle, and N content per cm needle in the 1969 flush, as influenced by sampling date and N treatment.

	% N			N/needle			N/cm needle		
Source	df	ms x 10^{-6}	F	df	ms x 10^{-4}	F	df	ms x 10^{-7}	F
Treatment (A)	2	43,695	24.60***	2	8,969	4.84*	2	10,305	6.34*
Linear	1	65,969	37.14***	1	17,505	9.44*	1	18,022	11.09**
Quadratic	1	21,420	12.06**	1	432	2.33	1	2,587	1.59
Error (a)	9	1,776		9	1,854		9	1,625	
Time (B)	13	56,558	23.34***	13	10,229	37.28***	13	7,085	17.54***
A x B	26	3,062	1.26	26	298	1.09	26	334	0.83
Error (b)	54	2,423		52	2,744		52	404	

Table 40. Analysis of variance of N concentration (% N), N content per needle, and N content per cm needle in the 1970 flush, as influenced by sampling date and N treatment.

		% N		N/needle		N/cm needle	
Source	df	ms x 10^{-7}	F	ms x 10^{-5}	F	ms x 10^{-8}	F
Treatment (A)	2	41,376	1.63	9,943	0.80	33,501	2.20
Linear	1	7,117	0.28	894	0.07	2,999	0.20
Quadratic	1	75,636	2.99	18,993	1.53	64,003	4.21
Error (a)	9	25,329		12,408		15,198	
Time (B)	5	290,092	21.96***	132,783	35.96***	78,206	17.22
A x B	10	5,280	0.40	1,106	0.30	2,393	0.53
Error (b)	18	13,211		3,693		4,540	

Table 41. Analysis of variance of P concentration (% P), P content per needle, and P content per cm needle in the 1968 flush, as influenced by sampling date and N treatment.

		%P		P/needle		P/cm needle	
Source	df	ms x 10^{-7}	F	ms x 10^{-7}	F	ms x 10^{-10}	F
Treatment (A)	2	20,094	3.42	56,382	0.51	105,397	1.00
Linear	1	18,420	3.14	104,788	0.95	193,118	1.83
Quadratic	1	21,769	3.71	7,976	0.07	17,677	0.17
Error (a)	9	5,871		110,443		105,253	
Time (B)	7	1,772	2.77*	111,120	0.90	15,658	1.15
A x B	14	675	1.05	5,723	0.47	9.018	0.66
Error (b)	33	641		12,294		13,659	

Table 42. Analysis of variance of P concentration (% P), P content per needle, and P content per cm needle in the 1969 flush, as influenced by sampling date and N treatment.

	% P			P/needle			P/cm needle		
Source	df	ms x 10^{-7}	F	df	ms x 10^{-7}	F	df	ms x 10^{-10}	F
Treatment (A)	2	9,288	3.42	2	89,682	1.91	2	78,255	1.37
Linear	1	1,282	0.47	1	178,767	3.80	1	153,913	2.70
Quadratic	1	17,294	6.37*	1	597	0.01	1	2,597	0.05
Error (a)	9	2,714		9	4,700		9	57,054	
Time (B)	13	3,129	2.61**	13	178,118	33.68***	13	87,953	9.07***
A x B	26	860	0.72	26	3,890	0.74	26	7,888	0.81
Error (b)	54	1,198		52	5,289		52	9,706	

Table 43. Analysis of variance of P concentration (% P), P content per needle, and P content per cm needle in the 1970 flush, as influenced by sampling date and N treatment.

		% P		P/needle		P/cm needle	
Source	df	ms x 10^{-8}	F	ms x 10^{-6}	F	ms x 10^{-10}	F
Treatment (A)	2	16,477	0.71	1,800	0.54	62,507	1.31
Linear	1	12,636	0.54	1,339	0.40	36,438	0.77
Quadratic	1	20,319	0.86	2,261	0.68	88,576	1.86
Error (a)	9	23,509		3,329		47,537	
Time (B)	5	37,641	5.06**	19,040	34.20***	89,708	11.34***
A x B	10	2,915	0.39	246	0.44	6,664	0.84
Error (b)	18	7,445		557		7,911	

Table 44. Analysis of variance of Al concentration (ppm Al) and P to Al ratio in the 1968 flush, as influenced by sampling date and N treatment.

		ppm Al		P to Al ratio	
Source	df	ms	F	ms x 10^{-5}	F
Treatment (A)	2	131,870	2.51	247,860	4.57*
Linear	1	51,257	0.97	6,046	0.11
Quadratic	1	212,482	4.04	489,673	9.03*
Error (a)	9	52,635		54,269	
Time (B)	7	3,427	1.08	2,974	0.86
A x B	14	472	0.15	2,756	0.80
Error (b)	33	3,167		3,458	

Table 45. Analysis of variance of Al concentration (ppm Al) and P to Al ratio in the 1969 flush, as influenced by sampling date and N treatment.

		ppm Al		P to Al ratio	
Source	df	ms	F	ms x 10^{-4}	F
Treatment (A)	2	61,087	1.93	47,780	2.40
Linear	1	10,707	0.34	2,093	0.09
Quadratic	1	111,467	3.52	93,467	3.90
Error (a)	9	31,649		23,954	
Time (B)	13	47,214	25.49***	59,863	9.07***
A x B	26	937	0.51	1,038	0.16
Error (b)	54	1,852		6,603	

Table 46. Analysis of variance of Al concentration (ppm Al) and P to Al ratio in the 1970 flush, as influenced by sampling date and N treatment.

		ppm Al		P to Al ratio	
Source	df	ms	F	ms x 10^{-4}	F
Treatment (A)	2	11,528	1.26	21,814	1.71
Linear	1	3,849	0.42	134	0.10
Quadratic	1	19,208	2.09	42,284	3.31
Error (a)	9	9,181		12,773	
Time (B)	5	24,696	104.31***	69,528	18.08***
A x B	10	653	2.76*	409	0.11
Error (b)	18	237		3,846	

Table 47. Analysis of variance of the percentage of the total N derived from the fertilizer [a] for the 1968, 1969, and 1970 needle flushes, as influenced by sampling date and N treatment.

	% N from fertilizer								
	1968 needles			1969 needles			1970 needles		
Source	df	ms x 10^{-3}	F	df	ms x 10^{-3}	F	df	ms x 10^{-3}	F
Treatment (A)	1	816,712	29.33**	1	2,385,501	59.96***	1	750,497	110.93***
Error (a)	6	27,845		6	39,734		6	6,765	
Time (B)	6	3,111	1.39	12	11,618	3.67**	5	1,765	8.27**
A + B	6	3,257	1.45	12	3,079	0.97	5	463	2.17
Error (b)	16	2,241		29	3,163		12	214	

[a] The analysis of variance of percentage of total N derived from the fertilizer and ^{15}N atom percent differ only by a constant.

Table 48. Analyses of variance of μeq ^{15}N absorbed, for the 1968 flush, as influenced by sampling date and N treatment.

		μeq ^{15}N absorbed					
		per gram		per needle		per cm needle	
Source	df	ms x 10^{-4}	F	ms x 10^{-5}	F	ms x 10^{-8}	F
Treatment (A)	1	135,191	31.88**	47,220	21.40**	88,890	23.86*
Error (a)	6	4,241		2,206		3,726	
Time (B)	6	667	1.24	178	0.83	368	0.95
A + B	6	728	1.35	160	0.74	345	0.89
Error (b)	16	538		215		387	

Table 49. Analysis of variance of μeq ^{15}N absorbed, for the 1970 flush, as influenced by sampling date and N treatment.

		μeq ^{15}N absorbed					
		per gram		per needle		per cm needle	
Source	df	msx10^{-5}	F	msx10^{-6}	F	msx10^{-10}	F
Treatment(A)	1	1,057,241	93.76***	206,625	87.22***	5,571,461	86.97***
Error(a)	6	11,276		2,369		64,060	
Time(B)	5	3,405	8.02***	14,239	59.77***	67,493	13.08***
A + B	5	1,180	2.78	4,737	19.88***	22,023	4.27*
Error(b)	12	425		238		5,162	

Table 50. Analysis of variance of μeq ^{15}N absorbed, for the 1969 flush, as influenced by sampling date and N treatment.

		μeq ^{15}N absorbed					
		per gram		per needle		per cm needle	
Source	df	msx10^{-4}	F	msx10^{-5}	F	msx10^{-8}	F
Treatment(A)	1	429,241	79.52***	162,575	87.69***	276,625	73.84***
Error(a)	6	5,398		1,854		3,746	
Time(B)	12	6,004	7.95***	2,846	8.26***	3,892	7.04***
A + B	12	2,401	3.18**	1,472	4.27***	1,793	3.24**
Error(b)	27	755		345		553	

APPENDIX D

Changes in Soil ^{15}N Levels with Time

Table 51. Changes in the amount and distribution of fertilizer applied N in the litter and soil at 6, 12, 30, and 84 weeks after fertilization with ammonium sulphate.

		N applied at 56 kg/ha					
Time after application	Soil depth	N	^{15}N	N/plot	N from fertilizer		N recovered
weeks	cm	%	atom %	g	% of total N	meq	%
6	Litter	0.65	0.532	99	8.2	577	20.4
	0-10	0.050	0.423	462	2.6	851	30.1
	10-20	0.025	0.382	263	0.5	102	3.6
	20-30	0.025	0.381	265	0.5	94	3.3
	30-40	0.019	0.375	202	0.2	29	1.0
	40-50	0.025	0.380	274	0.4	87	3.1
	Total			1565		1740	61.5
12	Litter	0.73	0.505	110	6.8	539	19.0
	0-10	0.039	0.402	361	1.5	396	14.0
	10-20	0.025	0.382	265	0.5	103	3.6
	20-30	0.027	0.374	290	0.1	30	1.1
	30-40	0.022	0.371	234	0.0	0	0.0
	40-50	0.011	0.382	123	0.5	48	1.6
	Total			1383		1116	39.3
30	Litter	0.63	0.477	95	5.4	370	13.1
	0-10	0.038	0.401	348	1.5	370	13.1
	10-20	0.028	0.382	288	0.5	112	4.0
	20-30	0.026	0.372	271	0.0	10	0.3
	30-40	0.022	0.371	229	0.0	0	0.0
	40-50	0.019	0.371	214	0.0	0	0.0
	Total			1445		862	30.5
84	Litter	0.53	0.455	81	4.5	255	9.0
	0-10	0.045	0.397	412	1.3	385	13.6
	10-20	0.030	0.378	310	0.3	83	2.9
	20-30	0.028	0.376	299	0.2	51	1.8
	30-40	0.024	0.372	254	0.0	10	0.3
	40-50	0.018	0.372	200	0.0	9	0.3
	Total			1556		793	27.9

Table 51. extended

N applied to 224 kg/ha					
N	^{15}N	N/plot	N from fertilizer		N recovered
%	atom %	g	% of total N	meq	%
0.67	0.660	100	14.5	1034	9.1
0.052	0.523	479	7.5	2578	22.8
0.131	0.458	324	4.3	998	8.8
0.027	0.434	286	3.1	639	5.6
0.022	0.414	240	2.1	365	3.2
0.009	0.393	100	1.1	78	0.7
		1529		5692	50.2
0.74	0.596	113	11.2	930	8.2
0.042	0.444	388	3.6	1004	8.9
0.037	0.395	393	1.2	334	3.0
0.028	0.377	299	0.3	64	0.6
0.026	0.376	283	0.2	50	0.4
0.011	0.383	119	0.6	51	0.4
		1595		2433	21.5
0.66	0.573	100	10.2	726	6.4
0.041	0.441	382	3.5	947	8.4
0.030	0.408	314	1.8	412	3.6
0.028	0.385	291	0.7	144	1.3
0.025	0.378	275	0.3	68	0.6
0.009	0.373	106	0.1	7	0.1
		1468		2304	20.4
0.58	0.579	92	10.5	697	6.2
0.037	0.429	341	2.9	701	6.2
0.029	0.401	310	1.5	326	2.9
0.029	0.380	307	0.4	97	0.9
0.024	0.378	265	0.3	68	0.6
0.020	0.378	234	0.3	55	0.5
		1549		1944	17.3

APPENDIX E

Sampling of Ecosystem

Data

Statistical Analysis

Data

Table 52. Dry weight and N in the various components of the tree at harvesting.

Category	Sample Position	N	Dry weight	Total N
		%	g	g
	Tree 1 (Control)			
Foliage	Terminal - 1970	0.92	141	1.22
	Terminal - 1969	0.72	24	0.17
	Upper Crown - 1970	0.96	1816	17.38
	Upper Crown - 1969	0.71	107	0.76
	Lower Crown - 1970	0.99	1505	14.93
	Lower Crown - 1969	0.78	169	1.31
Bud	Upper Crown	0.65	38	0.25
	Lower Crown	0.58	26	0.15
Branches	Upper Crown-1969-70	0.30	875	2.60
	Upper Crown-pre-1969	0.20	374	0.77
	Lower Crown-1969-70	0.28	731	2.08
	Lower Crown-pre-1969	0.17	2501	4.20
	Dead	0.14	2413	3.40
Stem	Bark	0.17	12,604	21.93
	Wood - 1969-70	0.08	7,882	6.23
	Wood - pre-1969	0.08	28,664	21.78
Roots	Inner fine	0.37	306	1.12
	Inner large	0.18	3,348	6.13
	Outer fine	0.43	267	1.15
	Outer large	0.21	752	1.59
	Tap fine	0.37	36	0.13
	Tap large	0.14	3,013	4.16
	Stump	0.10	7,413	7.26

Table 52. continued

Sample Category	Position	N	Dry weight	Total N
		%	g	g
		Tree 2 (Control)		
Foliage	Terminal - 1970	0.86	202	1.74
	Terminal - 1969	-	-	-
	Upper Crown - 1970	0.92	1,497	13.83
	Upper Crown - 1969	0.65	7	0.05
	Lower Crown - 1970	0.96	3,290	31.75
	Lower Crown - 1969	0.74	403	2.97
Buds	Upper Crown	0.72	31	0.22
	Lower Crown	0.59	43	0.25
Branches	Upper Crown-1969-70	0.29	869	2.51
	Upper Crown-pre-1969	-	-	-
	Lower Crown-1969-70	0.30	1,858	5.65
	Lower Crown-pre-1969	0.16	3,949	6.20
	Dead	0.16	3,163	4.97
Stem	Bark	0.19	14,382	27.18
	Wood-1969-70	0.08	16,036	13.15
	Wood-pre-1969	0.09	30,182	26.26
Roots	Inner fine	0.40	329	1.33
	Inner large	0.19	3,468	6.62
	Outer fine	0.46	386	1.76
	Outer large	0.24	2,451	5.98
	Tap fine	0.36	112	0.40
	Tap large	0.14	7,093	9.85
	Stump	0.14	5,500	7.48

Table 52. continued

Category	Sample Position	N	Dry weight	Total N
		%	g	g
	Tree 3 (Control)			
Foliage	Terminal - 1970	0.97	264	2.56
	Terminal - 1969	0.75	11	0.08
	Upper Crown - 1970	0.93	1,642	15.32
	Upper Crown - 1969	-	-	-
	Lower Crown - 1970	0.94	2,598	24.34
	Lower Crown - 1969	0.90	179	1.60
Buds	Upper Crown	0.68	45	0.31
	Lower Crown	0.74	33	0.24
Branches	Upper Crown-1969-70	0.33	731	2.43
	Upper Crown-pre-1969	-	-	-
	Lower Crown-1969-70	0.32	1,109	3.52
	Lower Crown-pre-1969	0.16	3,085	5.06
	Dead	0.16	2,380	3.83
Stem	Bark	0.17	14,095	23.96
	Wood-1969-70	0.06	13,982	8.26
	Wood-pre-1969	0.09	32,582	28.35
Roots	Inner fine	0.56	860	4.83
	Inner large	0.24	3,437	8.39
	Outer fine	0.58	1,847	10.77
	Outer large	0.32	1,793	5.74
	Tap fine	0.34	104	0.36
	Tap large	0.16	1,721	2.82
	Stump	0.11	9,789	11.06

Table 52. continued

Category	Sample Position	N	Dry weight	Total N
		%	g	g
		Tree 4 (Control)		
Foliage	Terminal - 1970	0.86	158	1.37
	Terminal - 1969	-	-	-
	Upper Crown - 1970	0.85	2,224	18.99
	Upper Crown - 1969	0.63	50	0.32
	Lower Crown - 1970	0.92	1,896	17.48
	Lower Crown - 1969	0.66	211	1.38
Buds	Upper Crown	0.66	38	0.25
	Lower Crown	0.71	26	0.19
Branches	Upper Crown-1969-70	0.26	815	2.11
	Upper Crown-pre-1969	-	-	-
	Lower Crown-1969-70	0.25	1,149	2.90
	Lower Crown-pre-1969	0.16	2,218	3.50
	Dead	0.21	2,995	6.29
Stem	Bark	0.17	12,722	21.50
	Wood-1969-70	0.07	10,973	7.46
	Wood-pre-1969	0.07	32,301	21.96
Roots	Inner fine	0.46	540	2.48
	Inner large	0.12	3,853	4.74
	Outer fine	0.42	366	1.54
	Outer large	0.19	1,289	2.40
	Tap fine	0.34	49	0.16
	Tap large	0.16	305	0.50
	Stump	0.11	10,010	11.01

Table 52. continued

Sample Category	Position	N %	N atom %	Dry weight g	Total N g	N from fertilizer % of total N	N from fertilizer meq	N recovered %
		Tree 5 (Low-N 56 kg N/ha)						
Foliage	Terminal - 1970	0.82	0.479	209	1.71	5.6	6.9	0.24
	Terminal - 1969	-	-	-	-	-	-	-
	Upper Crown - 1970	0.93	0.466	2,906	27.14	5.0	96.8	3.42
	Upper Crown - 1969	0.69	0.387	52	0.36	1.1	0.3	0.01
	Lower Crown - 1970	0.88	0.466	2,862	25.16	5.0	89.7	3.17
	Lower Crown - 1969	0.61	0.455	14	0.08	4.4	0.3	0.01
Buds	Upper Crown	0.67	0.477	61	0.41	5.5	1.6	0.06
	Lower Crown	0.60	0.466	30	0.18	4.9	0.6	0.02
Branches	Upper Crown-1969-70	0.29	0.464	1,638	4.83	4.8	16.6	0.59
	Upper Crown-pre-1969	0.20	0.454	496	0.97	4.3	3.0	0.11
	Lower Crown-1969-70	0.28	0.465	1,385	3.86	4.8	13.4	0.47
	Lower Crown-pre-1969	0.16	0.444	5,032	8.10	3.8	22.0	0.78
	Dead	0.16	0.406	2,494	3.89	1.9	5.4	0.19
Stem	Bark	0.18	0.419	13,399	23.98	2.4	41.6	1.47
	Wood-1969-70	0.08	0.465	13,936	10.59	4.8	36.3	1.28
	Wood-pre-1969	0.07	0.410	35,496	25.91	2.1	38.5	1.36
Roots	Inner fine	0.34	0.456	431	1.45	4.4	4.6	0.16
	Inner large	0.20	0.428	4,593	9.37	3.0	20.2	0.71
	Outer fine	0.44	0.387	793	3.50	1.0	2.5	0.09
	Outer large	0.24	0.394	1,187	2.86	1.3	2.7	0.10
	Tap fine	0.26	0.445	130	0.37	3.9	0.9	0.03
	Tap large	0.13	0.424	3,052	3.91	2.8	7.8	0.28
	Stump	0.10	0.401	9,702	10.19	1.7	12.2	0.43

Table 52. continued

Sample Category	Position	N %	N atom T	Dry weight g	Total N g	N from fertilizer % of total N	N from fertilizer meq	N recovered %
			Tree 6 (Low-N 56 kg N/ha)					
Foilage	Terminal - 1970	0.88	0.429	171	1.50	3.2	3.4	0.12
	Terminal - 1969	0.82	0.428	16	0.13	3.1	0.3	0.01
	Upper Crown - 1970	0.93	0.422	2,286	21.24	2.8	42.7	1.51
	Upper Crown - 1969	0.80	0.425	250	2.00	3.0	4.2	0.15
	Lower Crown - 1970	0.96	0.411	3,337	31.97	2.3	51.9	1.84
	Lower Crown - 1969	0.78	0.429	156	1.21	3.2	2.7	0.10
Buds+	Upper Crown	0.76	0.423	74	0.56	2.8	1.1	0.04
	Lower Crown							
Branches	Upper Crown-1969-70	0.33	0.423	1,295	4.25	2.8	8.4	0.30
	Upper Crown-pre-1969	0.23	0.420	435	1.00	2.6	1.9	0.07
	Lower Crown-1969-70	0.31	0.423	1,504	4.68	2.8	9.3	0.33
	Lower Crown-pre-1969	0.18	0.413	4,622	8.32	2.2	13.5	0.48
	Dead	0.15	0.405	2,931	4.34	1.9	5.8	0.21
Stem	Bark	0.18	0.384	14,956	27.67	0.7	13.7	0.48
	Wood-1969-70	0.07	0.462	15,258	10.68	4.7	35.5	1.26
	Wood-pre-1969	0.08	0.396	42,909	32.61	1.4	32.3	1.14
Roots	Inner fine	0.43	0.507	269	1.16	6.9	5.7	0.20
	Inner large	0.24	0.419	3,849	9.08	2.6	16.7	0.59
	Outer fine	0.46	0.385	813	3.74	0.9	2.4	0.08
	Outer large	0.28	0.394	2,446	6.95	1.3	6.6	0.23
	Tap fine	0.31	0.390	72	0.22	1.1	0.2	0.01
	Tap large	0.15	0.394	5,866	8.62	1.3	9.2	0.29
	Stump	0.11	0.394	11,522	13.02	1.3	12.4	0.44

+ Sample accidently combined

Table 52. continued

Sample								
Category	Position	N	N	Dry weight	Total N	N from fertilizer		N recovered
		%	atom %	g	g	% of total N	meq	%
		Tree 7 (Low-N 56 kg N/ha)						
Foliage	Terminal - 1970	0.95	0.428	239	2.27	3.2	5.1	0.18
	Terminal - 1969	0.79	0.423	14	0.11	2.9	0.2	0.01
	Upper Crown - 1970	0.90	0.423	1,185	10.64	2.9	21.8	0.77
	Upper Crown - 1969	0.72	0.426	100	0.72	3.0	1.5	0.06
	Lower Crown - 1970	0.87	0.423	2,086	18.23	2.9	37.3	1.32
	Lower Crown - 1969	0.71	0.461	513	3.66	4.7	12.4	0.44
Buds	Upper Crown	0.79	0.428	19	0.15	3.1	0.3	0.01
	Lower Crown	0.67	0.421	35	0.24	2.7	0.5	0.02
Branches	Upper Crown-1969-70	0.34	0.426	628	2.14	2.9	4.5	0.16
	Upper Crown-pre-1969	-	-	-	-	-	-	-
	Lower Crown-1969-70	0.30	0.419	1,404	4.17	2.5	7.6	0.27
	Lower Crown-pre-1969	0.19	0.409	3,333	6.37	2.1	9.4	0.33
	Dead	0.17	0.402	2,167	3.73	1.7	4.6	0.16
Stem	Bark	0.18	0.393	11,350	20.88	1.1	17.0	0.60
	Wood-1969-70	0.09	0.423	11,777	10.60	2.7	20.6	0.73
	Wood-pre-1969	0.07	0.393	34,864	23.71	1.2	21.0	0.74
Roots	Inner fine	0.35	0.434	350	1.22	3.3	2.9	0.10
	Inner large	0.19	0.427	3,384	6.43	2.9	13.6	0.48
	Outer fine	0.42	0.381	719	3.00	0.7	1.5	0.05
	Outer large	0.22	0.386	2,279	5.06	0.9	3.4	0.12
	Tap fine	0.28	0.394	35	0.10	1.3	0.1	0.00
	Tap large	0.16	0.386	1,737	2.73	0.9	1.8	0.06
	Stump	0.11	0.390	11,953	13.63	1.1	11.1	0.39

Table 52. continued

Sample								
Category	Position	N	^{15}N	Dry weight	Total N	N from fertilizer		N recovered
		%	atom %	g	g	% of total N	meq	%
		Tree 8 (Low-N 56 kg N/ha)						
Foliage	Terminal - 1970	0.88	0.462	152	1.33	4.8	4.5	0.16
	Terminal - 1969	0.69	0.432	61	0.42	3.3	1.0	0.04
	Upper Crown - 1970	0.83	0.456	1,750	14.56	4.5	46.8	1.65
	Upper Crown - 1969	0.66	0.463	224	1.47	4.8	5.1	0.18
	Lower Crown - 1970	0.79	0.451	2,588	20.55	4.3	62.4	2.21
	Lower Crown - 1969	0.65	0.462	171	1.11	4.8	3.8	0.13
Buds	Upper Crown	0.66	0.453	40	0.27	4.3	0.8	0.03
	Lower Crown	0.71	0.452	25	0.18	4.3	0.5	0.02
Branches	Upper Crown-1969-70	0.32	0.450	834	2.64	4.1	7.8	0.27
	Upper Crown-pre-1969	0.22	0.444	191	0.43	3.8	1.2	0.04
	Lower Crown-1969-70	0.30	0.447	1,127	3.42	4.0	9.7	0.34
	Lower Crown-pre-1969	0.17	0.439	3,085	5.37	3.6	13.7	0.48
	Dead	0.15	0.399	2,584	3.90	1.6	4.4	0.16
Stem	Bark	0.17	0.408	12,322	21.07	1.9	28.3	1.00
	Wood-1969-70	0.08	0.451	14,175	11.62	4.1	34.1	1.21
	Wood-pre-1969	0.08	0.406	34,484	27.24	1.9	36.6	1.29
Roots	Inner fine	0.43	0.450	445	1.91	4.1	5.6	0.20
	Inner large	0.17	0.422	2,843	4.75	2.7	9.2	0.33
	Outer fine	0.40	0.381	157	0.63	0.7	0.3	0.01
	Outer large	0.24	0.389	217	0.52	1.1	0.4	0.01
	Tap fine	0.40	0.392	38	0.15	1.2	0.1	0.00
	Tap large	0.16	0.417	1,360	2.27	2.5	3.9	0.14
	Stump	0.10	0.399	11,239	11.01	1.6	12.5	0.44

Table 52. continued

Sample								
Category	Position	N	^{15}N	Dry weight	Total N	N from fertilizer		N recovered
		%	atom %	g	g	% of total N	meq	%
		Tree 9 (High-N 224 kg N/ha)						
Foliage	Terminal - 1970	0.86	0.651	210	1.81	14.1	18.3	0.16
	Terminal - 1969	-	-	-	-	-	-	-
	Upper Crown - 1970	0.90	0.648	1,185	10.63	14.0	106.2	0.94
	Upper Crown - 1969	-	-	-	-	-	-	-
	Lower Crown - 1970	0.95	0.649	1,900	18.07	14.0	181.2	1.60
	Lower Crown - 1969	0.62	0.609	28	0.17	12.1	1.5	0.01
Buds	Upper Crown	0.90	0.654	20	0.18	14.2	1.8	0.02
	Lower Crown	0.82	0.641	18	0.14	13.6	1.4	0.01
Branches	Upper Crown-1969-70	0.34	0.641	507	1.72	13.6	16.7	0.15
	Upper Crown-pre-1969	-	-	-	-	-	-	-
	Lower Crown-1969-70	0.33	0.635	696	2.31	13.3	21.9	0.19
	Lower Crown-pre-1969	0.19	0.610	1,288	2.46	12.0	21.1	0.18
	Dead	0.18	0.533	1,048	1.90	8.2	11.2	0.10
Stem	Bark	0.19	0.478	11,929	22.90	5.4	87.6	0.77
	Wood-1969-70	0.11	0.606	7,167	7.96	11.8	67.0	0.59
	Wood-pre-1969	0.12	0.490	27,404	33.16	6.0	143.0	1.26
Roots	Inner fine	0.43	0.633	310	1.32	13.2	12.5	0.11
	Inner large	0.27	0.594	2,878	7.80	11.2	62.6	0.55
	Outer fine	0.58	0.448	397	2.29	4.0	6.5	0.06
	Outer large	0.33	0.467	724	2.41	4.9	8.5	0.07
	Tap fine	0.40	0.469	152	0.60	5.0	2.2	0.02
	Tap large	0.17	0.468	3,375	5.77	4.8	19.8	0.17
	Stump	0.08	0.475	6,855	5.28	5.3	20.1	0.18

Table 52. continued

Sample								
Category	Position	N	^{15}N	Dry weight	Total N	N from fertilizer		N recovered
		%	atom %	g	g	% of total N	meq	%
		Tree 10 (High-N 224 kg N/ha)						
Foliage	Terminal - 1970	0.90	0.774	264	2.36	20.2	34.2	0.30
	Terminal - 1969	-	-	-	-	-	-	-
	Upper Crown - 1970	0.88	0.755	1,526	13.37	19.3	184.1	1.63
	Upper Crown - 1969	0.71	0.742	14	0.10	18.6	1.3	0.01
	Lower Crown - 1970	0.90	0.744	2,086	18.86	18.7	252.3	2.23
	Lower Crown - 1969	0.71	0.744	100	0.71	18.7	9.5	0.08
Buds	Upper Crown	0.71	0.754	37	0.27	19.2	3.6	0.03
	Lower Crown	0.72	0.746	33	0.24	18.8	3.2	0.03
Branches	Upper Crown-1969-70	0.29+	0.727+	1,004	2.95	17.8	37.6	0.33
	Upper Crown-pre-1969	-	-	-	-	-	-	-
	Lower Crown-1969-70	0.29+	0.727+	1,299	3.82	17.8	48.6	0.43
	Lower Crown-pre-1969	0.18	0.696	1,745	3.12	16.3	36.3	0.32
	Dead	0.16	0.548	1,727	2.85	9.0	18.2	0.16
Stem	Bark	0.17	0.544	13,209	21.93	8.6	135.0	1.19
	Wood-1969-70	0.08	0.723	13,348	10.42	17.6	130.8	1.16
	Wood-pre-1969	0.09	0.522	28,381	24.69	7.6	134.5	1.19
Roots	Inner fine	0.49	0.648	356	1.75	13.9	17.4	0.15
	Inner large	0.23	0.618	2,460	5.63	12.4	50.0	0.44
	Outer fine	0.57	0.475	615	3.50	5.3	13.4	0.12
	Outer large	0.30	0.499	914	2.78	6.5	13.0	0.11
	Tap fine	0.39	0.531	240	0.93	8.1	5.4	0.05
	Tap large	0.15	0.540	3,877	5.78	8.6	35.3	0.31
	Stump	0.10	0.513	7,760	7.84	7.2	40.4	0.36

+ sample accidently combined prior to analysis

Table 52. continued

Sample								
Category	Position	N	^{15}N	Dry weight	Total N	N from fertilizer		N recovered
		%	atom %	g	g	% of total N	meq	%
		Tree 11 (High-N 224 kg N/ha)						
Foliage	Terminal - 1970	0.88	0.730	216	1.90	18.0	24.4	0.22
	Terminal - 1969	0.71	0.739	44	0.31	18.5	4.1	0.04
	Upper Crown - 1970	0.84	0.708	1,182	9.98	17.0	120.8	1.07
	Upper Crown - 1969	-	-	-	-	-	-	-
	Lower Crown - 1970	0.80	0.709	3,390	27.12	17.0	329.4	2.91
	Lower Crown - 1969	0.73	0.724	102	0.74	17.7	9.4	0.08
Buds	Upper Crown	0.76	0.713	32	0.24	17.2	3.0	0.03
	Lower Crown	0.81	0.707	48	0.39	16.9	4.6	0.04
Branches	Upper Crown-1969-70	0.33	0.725	985	3.24	17.7	41.0	0.36
	Upper Crown-pre-1969	-	-	-	-	-	-	-
	Lower Crown-1969-70	0.32	0.692	969	3.12	16.0	35.8	0.32
	Lower Crown-pre-1969	0.18	0.640	2,858	5.06	13.5	48.8	0.43
	Dead	0.17	0.513	1,300	2.20	7.2	11.3	0.10
Stem	Bark	0.18	0.501	12,672	22.55	6.5	104.6	0.92
	Wood-1969-70	0.09	0.676	15,064	13.55	15.2	147.6	1.30
	Wood-pre-1969	0.09	0.507	32,704	28.45	6.9	139.8	1.24
Roots	Inner fine	0.43	0.565	202	0.87	9.8	6.1	0.05
	Inner large	0.25	0.547	2,976	7.56	8.9	48.1	0.43
	Outer fine	0.49	0.446	221	1.09	3.9	3.0	0.03
	Outer large	0.30	0.459	2,020	5.98	4.6	19.4	0.17
	Tap fine	0.44	0.504	103	0.45	6.8	2.2	0.02
	Tap large	0.16	0.530	3,197	5.28	8.1	30.4	0.27
	Stump	0.14	0.487	9,728	13.13	5.9	55.7	0.49

Table 52. continued

Sample								
Category	Position	N	^{15}N	Dry weight	Total N	N from fertilizer		N recovered
		%	atom %	g	g	% of total N	meq	%
		Tree 12 (High-N 224 kg N/ha)						
Foliage	Terminal - 1970	0.86	0.710	304	2.60	17.0	31.6	0.28
	Terminal - 1969	0.65	0.723	28	0.18	17.7	2.3	0.02
	Upper Crown - 1970	0.83	0.685	2,015	16.78	15.8	189.6	1.68
	Upper Crown - 1969	0.75	0.725	467	3.52	17.8	44.8	0.40
	Lower Crown - 1970	0.88	0.690	3,133	27.54	16.1	316.0	2.79
	Lower Crown - 1969	0.73	0.719	463	3.36	17.5	42.0	0.37
Buds	Upper Crown	0.77	0.700	35	0.27	16.5	3.1	0.03
	Lower Crown	0.83	0.693	39	0.33	16.2	3.8	0.03
Branches	Upper Crown-1969-70	0.30	0.681	1,278	3.87	15.5	43.0	0.38
	Upper Crown-pre-1969	0.19	0.676	159	0.30	15.3	3.3	0.03
	Lower Crown-1969-70	0.31	0.677	1,619	4.97	15.3	54.5	0.48
	Lower Crown-pre-1969	0.18	0.613	5,216	9.49	12.2	82.5	0.73
	Dead	0.16	0.508	3,742	5.99	7.0	29.8	0.26
Stem	Bark	0.18	0.529	12,628	22.86	7.9	128.7	1.14
	Wood-1969-70	0.09	0.670	13,413	12.07	15.0	128.9	1.14
	Wood-pre-1969	0.10	0.486	31,785	33.06	5.8	137.9	1.22
Roots	Inner fine	0.41	0.631	949	3.96	13.0	36.9	0.33
	Inner large	0.22	0.632	4,990	11.13	13.1	104.2	0.92
	Outer fine	0.56	0.423	479	2.66	2.7	5.3	0.05
	Outer large	0.28	0.481	757	2.13	5.6	8.6	0.08
	Tap fine	0.29	0.496	173	0.50	6.3	2.3	0.02
	Tap large	0.17	0.521	2,685	4.59	7.6	25.0	0.22
	Stump	0.18	0.520	11,397	20.74	7.6	112.2	0.99

Statistical Analysis

Table 53. Analyses of variances of N concentration (% N) and ^{15}N atom percent in the 1970 foliage at harvesting.

Source	% N			^{15}N atom %[a]		
	df	ms x 10^{-6}	F	df	ms x 10^{-7}	F
Treatment (A)	2	8,807	2.46	1	4,100,300	104.54***
Error (a)	9	3,580	0.66	6	39,224	
Crown Position (B)	2	1,074	0.81	2	5,167	17.66***
A x B	4	1,317		2	472	1.61
Error (b)	18	1,617		12	293	

*** Significant at 0.1 percent level.

[a] Control treatment is not included in ^{15}N atom percent ANOVA.

Table 54. Analysis of variances of N concentration (% N) and ^{15}N atom percent in the branches[a] at harvesting.

Source	% N			^{15}N atom %[b]		
	df	ms x 10^{-7}	F	df	ms x 10^{-7}	F
Treatment (A)	2	11,738	2.07	1	346,944	151.32***
Error (a)	9	5,669		6	22,928	
Branches (B)	3	743,810	239.52**	3	177,119	63.11***
A x B	6	2,544	0.82	3	71,046	25.32***
Error (b)	27	3,106		18	2,806	

** Significant at 1 percent level.

*** Significant at 0.1 percent level.

[a] Does not include upper crown, pre-1969 branches as these were often missing.

[b] The control treatment is not included in ^{15}N atom percent ANOVA.

Table 55. Analysis of variance of stem ^{15}N atom percent, as influenced by fertilizer treatment and components.

Source	df	ms x 10^{-6}	F
Treatments (A)	1	124,843	89.46***
Error (a)	6	1,395	
Component (B)	2	29,390	103.07***
A x B	2	8,374	29.37***
Error (b)	12	285	

*** Significant at 0.1 percent level.

Table 56. Analysis of variance of N concentration (% N) and ^{15}N atom percent in the roots at harvesting.

Source	% N			^{15}N atom %[a]		
	df	ms x 10^{-6}	F	df	ms x 10^{-6}	F
Treatment (A)	2	17,525	4.11	1	177,190	113.50***
Error (a)	9	4,262		6	1,561	
Roots (B)	6	234,160	158.52***	6	15,606	39.39***
A x B	12	2,432	1.65	6	3,074	7.76***
Error (b)	54	1,477		36	396	

*** Significant at 0.1 percent level.

[a] The control treatment is not included in ^{15}N atom percent ANOVA.

Table 57. Analysis of variance of N concentration and ^{15}N atom percent in ground vegetation at harvesting.

Source	% N			^{15}N atom %[a]		
	df	ms x 10^{-5}	F	df	ms x 10^{-6}	F
Treatment (A)	2	15,023	4.84*	1	26,002	0.50
Error (a)	9	3,103		6	52,312	
Subplot (B)	1	3,286	1.03	1	57,002	1.13
A x B	2	4,162	1.31	1	9,072	0.18
Error (b)	9	3,188		6	50,331	

* Significant at five percent level.

[a] Control treatment not included in ^{15}N atom percent ANOVA.

Table 58. Analysis of variance of dry weight (g/m^2), N concentration (% N), and N content (mg/m^2) in litter samples collected at harvesting.

Source	df	Dry Weight		% N		N Content	
		ms	F	ms	F	ms x 10^{-3}	F
Treatment	2	187,403	1.77	16,018	6.06*	25,031	3.54
Exp. Error	9	105,811	1.28	2,645	3.10*	7,061	5.18**
Sampling Error	12	82,884		852		1,364	

* Significant at 5 percent level.

** Significant at 1 percent level.

Table 59. Nitrogen in the soils at harvesting as influenced by treatment and soil depth.

Treatment	Plot number	Soil depth	Total N	^{15}N	Bulk density	Total N/plot	N from fertilizer		N recovered
							% of		
		cm	%	atom %	g/cm^3	g	total	meq	%
Low N	5	0-10	0.048	0.395	1.28	432	1.19	368	13.00
		10-20	0.035	0.380	1.44	352	0.45	112	3.97
		20-30	0.030	0.377	1.54	329	0.30	70	2.47
		30-40	0.026	0.372	1.49	274	0.05	10	0.34
		40-50	0.020	0.372	1.54	220	0.05	8	0.27
		Total				1607		568	20.05
	6	0-10	0.037	0.401	1.38	364	1.49	387	13.67
		10-20	0.028	0.380	1.47	287	0.45	91	3.23
		20-30	0.028	0.379	1.49	294	0.40	83	2.94
		30-40	0.024	0.373	1.51	255	0.10	18	0.64
		40-50	0.017	0.371	1.54	183	0.00	0	0.00
		Total				1383		579	20.48
	7	0-10	0.058	0.402	1.29	525	1.54	577	20.39
		10-20	0.030	0.377	1.50	320	0.30	68	2.41
		20-30	0.027	0.375	1.55	296	0.20	42	1.48
		30-40	0.020	0.371	1.50	213	0.00	0	0.00
		40-50	0.017	0.373	1.54	181	0.10	13	0.45
		Total				1535		700	24.73
	8	0-10	0.037	0.389	1.26	329	0.89	210	7.41
		10-20	0.026	0.377	1.51	282	0.30	60	2.12
		20-30	0.027	0.372	1.44	276	0.05	10	0.35
		30-40	0.027	0.372	1.44	275	0.05	10	0.34
		40-50	0.020	0.373	1.57	216	0.10	15	0.54
		Total				1378		305	10.76

Table 59. continued

Treatment	Plot number	Soil depth	Total N	^{15}N	Bulk density	Total N/plot	N From fertilizer		N recovered
		cm	%	atom %	g/cm³	g	% of total	meq	%
	All Plots	50-60	0.0100	0.371	1.59	112	0.00	0	0.00
		60-80	0.0042	0.372	1.61	96	0.05	3	0.12
		80-100	0.0034	0.378	1.71	82	0.35	20	0.72
		100-120	0.0065	0.371	1.74	160	0.00	0	0.00
		120-140	0.0065	0.371	1.89	172	0.00	0	0.00
		140-160	0.0092	0.373	1.66	214	0.10	15	0.54
		160-180	0.0110	0.373	1.68	260	0.10	19	0.65
		180-200	0.0108	0.371	1.65	252	0.00	0	0.00
		Total				1348		47	2.03
High N	9	0-10	0.033	0.419	1.37	317	2.37	538	4.76
		10-20	0.028	0.393	1.52	297	1.19	252	2.23
		20-30	0.030	0.376	1.57	331	0.25	59	0.52
		30-40	0.026	0.375	1.58	293	0.20	41	0.37
		40-50	0.020	0.379	1.63	225	0.40	64	0.56
		Total				1463		954	8.44
	10	0-10	0.039	0.449	1.22	338	3.52	850	7.52
		10-20	0.028	0.398	1.47	292	1.34	270	2.47
		20-30	0.027	0.384	1.49	279	0.64	128	1.14
		30-40	0.020	0.378	1.52	219	0.35	54	0.48
		40-50	0.018	0.376	1.59	206	0.25	36	0.32
		Total				1334		1347	11.93
	11	0-10	0.037	0.418	1.30	342	2.33	569	5.03
		10-20	0.032	0.399	1.50	342	1.39	340	3.00
		20-30	0.036	0.382	1.39	353	0.55	137	1.21
		30-40	0.028	0.384	1.55	306	0.64	142	1.25
		40-50	0.024	0.380	1.58	262	0.45	84	0.70
		Total				1607		1272	11.23

Table 59. continued

Treatment	Plot number	Soil depth	Total N	^{15}N	Bulk density	Total N/plot	N from fertilizer		N recovered
		cm	%	atom %	g/cm^3	g	% of total	meq	%
	12	0-10	0.039	0.436	1.34	368	3.22	848	7.50
		10-20	0.029	0.411	1.48	307	1.98	434	3.84
		20-30	0.024	0.378	1.55	264	0.35	65	0.58
		30-40	0.021	0.375	1.60	241	0.20	34	0.30
		40-50	0.022	0.375	1.56	245	0.20	35	0.31
		Total				1425		1416	12.53
	All Plots	50-60	0.0073	0.377	1.59	82	0.30	17	0.15
		60-80	0.0098	0.375	1.61	232	0.20	32	0.28
		80-100	0.0030	0.374	1.71	72	0.15	8	0.07
		100-120	0.0033	0.377	1.74	82	0.30	17	0.15
		120-140	0.0025	0.374	1.89	66	0.15	7	0.06
		140-160	0.0086	0.371	1.66	202	0.00	0	0.00
		160-180	0.0084	0.371	1.68	200	0.00	0	0.00
		180-200	0.0083	0.371	1.65	194	0.00	0	0.00
		Total				1130		81	0.71

APPENDIX F

Tree Measurements in December 1970

Table 60. Mensurational data on sample trees felled in December 1970.

	Fertilizer Treatment												
	Control No N				Low-N 56 kg N/ha				High-N 224 kg N/ha				Mean
	1	2	3	4	5	6	7	8	9	10	11	12	
Height (m)	13.77	13.80	13.59	13.16	14.22	14.63	14.15	13.74	13.77	14.25	14.00	13.08	13.88
Height measurement (m)	1.68	1.95	1.83	1.78	2.08	1.83	1.85	1.57	2.01	2.06	1.74	1.95	1.90
Diameter breast height (cm)	15.3	16.4	16.1	15.7	15.9	16.2	15.5	15.7	15.0	16.1	15.5	15.5	15.7
Basal area increment (cm^2/yrs)	9.3	8.9	10.1	9.9	12.2	12.6	8.4	10.3	5.6	9.7	10.4	9.9	9.8
CS area increment at 6.5m (cm^2)[a]	8.0	13.0	10.3	8.8	12.4	10.8	9.2	9.4	3.4	9.3	8.1	10.7	9.4
Volume OB (dm^3)	124.54	152.10	147.85	137.41	160.64	161.67	147.43	137.30	123.54	148.97	133.78	123.54	141.56
Volume IB (dm^3)	78.38	92.49	93.12	90.57	112.12	110.17	103.57	94.00	76.23	92.97	89.83	93.74	93.93
Volume increment (dm^3/yr)	9.78	14.22	11.80	10.88	15.41	15.18	12.20	11.90	7.16	13.48	12.04	12.50	12.21
Crown length (m)	5.03	6.35	5.06	4.83	6.68	6.10	5.23	4.93	4.02	5.06	5.36	5.94	5.38
Crown radius (m)	2.02	2.13	1.85	1.92	2.07	2.12	2.02	1.92	1.62	1.65	1.72	2.27	1.94
Height to long-term sampling whorl (m)	10.06	9.60	9.70	9.65	9.86	10.36	10.13	10.26	10.16	9.91	10.13	9.14	9.91

[a] Increment in cross section area at 6.5 m above ground.

Table 61. Analysis of covariance of basal area breast height increment using pretreatment under-bark basal area and crown area as covariates.

Source	df	yy	ss (due)	ss (about)	df	ms	F
Treatment	2	8.1340					
Error (within)	9	26.0552	6.9797	19.0755	7	2.7251	
Treatment + Error(total)	11	34.1892	14.2572	19.9320	9		
Difference (treatment adjusted)				0.8566	2	0.4283	0.16

Table 62. Analysis of covariance of volume increment using pretreatment volume and crown area as covariates.

Source	df	yy	ss (due)	ss (about)	df	ms	F
Treatment	2	13.0708					
Error (within)	9	45.1970	26.0845	19.1125	7	2.7304	
Treatment + Error(total)	11	58.2678	38.6460	19.6218	9		
Difference (treatments adjusted)				0.5093	2	0.2546	0.09

Table 63. Analysis of covariance of height increment using pretreatment height and crown area as covariates.

Source	df	yy	ss (due)	ss (about)	df	ms	F
Treatment	2	0.0387					
Error (within)	9	0.2276	0.0322	0.1954	7	0.0279	
Treatment + Error(total)	11	0.2663	0.0167	0.2496	9		
Difference (treatments adjusted)				0.0542	2	0.0271	0.97

Table 64. Analysis of covariance of cross section area at 6.5 m above the ground using crown area as a covariate.

Source	df	yy	ss (due)	ss (about)	df	ms	F
Treatment	2	15.0488					
Error (within)	9	51.1748	34.3210	16.8538	8	2.1067	
Treatment + Error(total)	11	66.2236	47.0898	19.1338	10		
Difference (treatment adjusted)				2.2800	2	1.1400	0.54

APPENDIX G

Supplementary Experiment with Nitrate-ion Electrode

To ascertain if the nitrate-ion electrode was adequate for determining low levels of nitrate in soil, additions of 0.0, 3.1, and 6.2 ppm nitrate were made to two soil samples. Both soil samples were from the A_1 horizon of the Tavares sand at the experimental site; one being taken from 0 to 10 cm depth and the other from 40 to 50 cm. The experiment was run as a completely randomized design with three replications and with three determinations being made on every sample.

A soil solution ratio of 1:2 (using 25.0 g of air-dried, sieved soil) was used. The mixture was stirred for 30 minutes and readings made in the supernatent liquid. While making the readings the solution was stirred with a magnetic stirrer. The readings in the solution are given in Table 65 and should be multiplied by two to give ppm in the soil.

The analysis of variance (Table 66) indicated that nitrate additions and soils differed significantly. The soils x nitrate interaction was not significant. The sampling error, which is a measure of the variability of the determinations, was greater than the error due to treatment replications. Subdivision of the nitrate sum of squares indicated that there was a significant linear trend. The regression of nitrate measured in the supernatent (Y)

against nitrate additions (X) in ppm is

$$Y = 0.855 + 0.827\ X$$

Recovery of added nitrate was about 83 percent and the level in the untreated soil 0.9 percent.

The main problem with the method was poor reproducibility of the readings at low levels of nitrates. Meyers and Paul (1968) found that erratic results were eliminated by using a paddle stirrer in place of a magnetic type stirrer. Even considering all the errors, the answer obtained with low levels of nitrate (i.e., below 4 ppm in the supernatent) was within 1 ppm.

Table 65. Levels of nitrate in the supernatant liquid as influenced by nitrate addition and soil. Measurements made with a nitrate-ion electrode.

Soil Depth	Treatment[a]	Readings			Mean
	ppm NO_3^-				
0-10 cm	0.00	0.84	0.50	0.50	0.61
	0.00	1.10	0.46	0.80	0.79
	0.00	1.05	0.54	1.35	0.98
	1.55	2.05	2.80	1.55	2.13
	1.55	2.30	2.60	1.40	2.10
	1.55	1.90	2.40	1.80	2.03
	3.10	3.55	3.55	2.70	3.27
	3.10	3.20	3.60	2.30	3.03
	3.10	3.95	2.70	3.10	3.25
40-50 cm	0.00	0.90	0.64	1.15	0.90
	0.00	0.62	0.47	0.56	0.55
	0.00	1.05	1.40	0.90	1.12
	1.55	2.55	2.80	1.50	2.28
	1.55	2.35	2.90	1.80	2.35
	1.55	2.40	2.85	1.60	2.28
	3.10	3.45	4.00	3.20	3.55
	3.10	4.00	2.90	4.00	3.63
	3.10	3.70	3.75	3.30	3.58

[a] Treatments are given as ppm in the supernatant liquid. All figures should be doubled to give ppm in the soil.

Table 66. Analysis of variance of experiment to determine the recovery of added nitrate using the nitrate-ion electrode method.

Source	df	ms x 10^{-4}	F
Treatment	5	120,310	174.31***
Nitrate (A)	2	295,934	428.77***
Linear	1	590,848	586.07***
Quadratic	1	1,021	1.48
Soil (B)	1	7,004	10.15**
A x B	2	1,338	1.94
Error	12	690	
Sampling Error	36	2,354	

** Significant at 1 percent level.

*** Significant at 0.1 percent level.

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BIOGRAPHICAL SKETCH

Donald James Mead was born in Raetihi, New Zealand on May 6, 1940. He attended Wanganui Technical College between the years 1953 and 1956. In 1957 he joined the New Zealand Forest Service and between 1958 and 1962 studied at Victoria University of Wellington, New Zealand. After gaining his Bachelor of Science (N.Z.) in botany he was awarded a scholarship by the New Zealand Forest Service to study forestry at Edinburgh University, Scotland. In 1964 he graduated Bachelor of Forestry Science (Edin.) and while there was awarded the 1963 Stebbing Commemorative Medal for Silviculture, and the 1964 Stewart McDougall prize for Forest Biology and the Elizabeth Sinclair Irvine prize in Forestry.

In 1965 Donald Mead joined the Soils and Tree Nutrition section of the New Zealand Forest Service, Forest Research Institute at Rotorua. In 1968 he was given leave to come to study for a Ph.D. at the University of Florida.

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Donald Mead is married to the former Tiffany Judith Thornley of Wellington, New Zealand, and has two children, Christopher and Diana.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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